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Cover photo: *Clitaetra irenae* female (Araneae, Nephilidae) from South Africa. Photo by Matjaž Kuntner.

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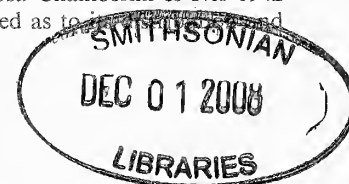
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A redescription of *Varacosa apothetica* (Wallace) (Araneae, Lycosidae)

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Abstract. *Lycosa apothetica* Wallace 1947 is redescribed as a member of the genus *Varacosa* Chamberlin & Ivie 1942 based on genitalic morphology. The species is freshly illustrated, and information is provided as to its life history and interesting characteristics.

Keywords: *Lycosa*, *Trochosa*, Florida spiders



Like many newly described members of the family Lycosidae Sundevall 1833 from the mid-20th century, *Lycosa apothetica* Wallace 1947 was originally described in the genus *Lycosa* Latreille 1804. Roewer (1955) placed the species in *Varacosa* Chamberlin & Ivie 1942 when he elevated this genus from its subgeneric status within *Trochosa* C.L. Koch 1847, but his reasons for doing so were not made clear. *Varacosa apothetica* was not part of Brady's (1980) *Trochosa avara* group nor was it treated as a member of *Varacosa* by Jiménez & Dondale (1988). Platnick (2008) therefore placed *V. apothetica* within *Trochosa* along with the rest of Roewer's *Varacosa* not included by Jiménez & Dondale (1988). Based on Wallace's illustrations (1947), it seemed likely that the species belonged to *Varacosa*. Wallace (1947) examined a total of 57 specimens from the Southeastern United States (8♂, 49♀♀) in his original description. Having examined most of the type material, I here support Roewer's (1955) combination *Varacosa apothetica* by showing that the species bears a prominent synapomorphy of *Varacosa*; i.e., the conspicuous anterior curvature of the transverse piece of the epigynum.

METHODS

Descriptions and drawings are based on specimens viewed in 70–75% ethanol under direct illumination. The epigynum was removed and cleared with clove oil, and the spermathecae were illustrated within this liquid. For clarity, palpal setae were omitted. Measurements reported here are those found in Wallace's (1947) original description of the species. Figure 8 reflects the collection localities of the specimens examined here as well as those included in Wallace (1947) that could not be located.

Abbreviations.—Male palpal structures: palea region (pr), tegular lobe (tl), embolus (emb), terminal apophysis (ta), median apophysis (ma), tegulum (tg). Female genitalic structures: head of spermathecae (hs), stalk of spermathecae (ss), fertilization ducts (fd). Body Dimensions: carapace width (CW), carapace length (CL), Eyes: posterior ocular quadrangle width (POQW), posterior ocular quadrangle length (POQL), posterior median eye width (PMEW), posterior lateral eye width (PLEW), clypeus height (CH). Palpal segments: palpal femur (PF), palpal patella (PP), palpal tibia (PT), palpal cymbium ♂ (PC), palpal tarsus & claw ♀ (PTC). Legs: femur (F1–4), patella (P1–4), tibia (Ti1–4), metatarsus (M1–4), tarsus (T1–4). Collections: American Museum of Natural History, New York (AMNH); Florida State Collection of Arthropods, Gainesville (FSCA).

TAXONOMY

Family Lycosidae Sundevall 1833
Genus *Varacosa* Chamberlin & Ivie 1942

Trochosa C.L. Koch 1848:95, in part. Brady 1980:168, in part. Platnick 2008, in part.

Trochosa (*Varacosa*) Chamberlin and Ivie 1942:36.

Varacosa: Roewer 1955:304. (Raised to generic status).

Jiménez & Dondale 1988:172.

Type species.—*Trochosa avara* Keyserling 1877, by original designation.

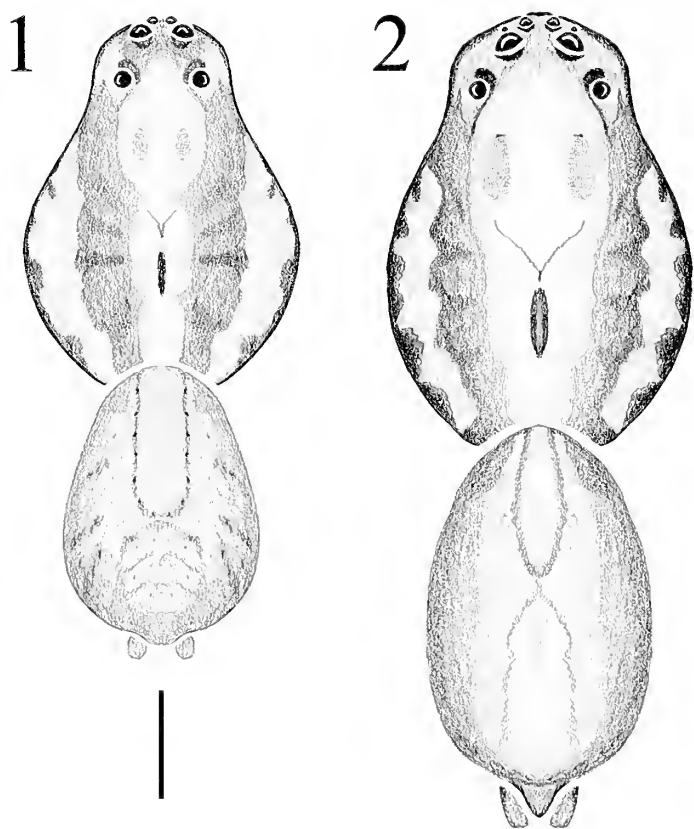
Varacosa apothetica (Wallace 1947)

Figures 1–7

Lycosa apothetica Wallace 1947:33, figs. 1, 2.

Varacosa apothetica Roewer 1955:306.

Type material examined.—*Varacosa apothetica*: allotype ♂ USA: Florida: Alachua County: 29°39'N, 082°19'W, 26 October 1937, H.K. Wallace (AMNH); *Lycosa apothetica*: holotype ♀ USA: Florida: Alachua County: Station 7B, 29°39'N, 082°19'W, 26 October 1937, H.K. Wallace (AMNH). Paratypes: U.S.A.: Florida: 2♀ Alachua County, Station 1, 29°39'N, 082°19'W, 19 January 1937, H.K. Wallace (FSCA); 1♀ same location, 29°39'N, 082°19'W, 30 January 1937 (FSCA); 2♀ Alachua County, Station 1B, 29°39'N, 082°19'W, 30 January 1937, H.K. Wallace (FSCA); 5♀ Alachua County, Station 1 vicinity, 29°39'N, 082°19'W, 30 January 1937 (FSCA); 2♀ same location, 29°39'N, 082°19'W, 19 April 1937 (FSCA); 1♀ same location, 29°39'N, 082°19'W, 22 January 1939, H.K. Wallace (FSCA); 2♀ Alachua County, Station 2 vicinity, 29°39'N, 082°19'W, 30 January 1937, H.K. Wallace (FSCA); 2♀ Alachua County: Station 7A, 29°39'N, 082°19'W, 7 February 1937 (FSCA); 2♀ Alachua County, Station 7B, 29°39'N, 082°19'W, 20 January 1937 (FSCA); 3♀ same location, 29°39'N, 082°19'W, 8 February 1937 (FSCA); 1♂2♀ same location, 29°39'N, 082°19'W, 26 May 1937 (FSCA); 1♀ Alachua County: Gainesville, 29°39'N, 082°19'W, 18 March 1938, W.J. Gertsch (FSCA); 1♂ Alachua County: pine flatwoods, 29°39'N, 082°19'W, 2 July 1938, C. Benton (FSCA); 1♀ Alachua County, 29°39'N, 082°19'W, 11 April 1933, H.K. Wallace (FSCA); 4♀ Alachua County, 29°39'N, 082°19'W, 15 February 1938, H.K. Wallace (FSCA); 3♀ Leon County, 30°26'N, 084°16'W, 16 March 1936, H.K. Wallace (FSCA). Georgia: 1♀ Turner County, 31°42'N, 083°39'W, 6 May 1937, H.K. Wallace (FSCA); No Locality:



Figures 1, 2.—Dorsal view of carapace and abdomen: 1. *Varacosa apothetica*, allotype male from Florida, USA; 2. *Lycosa apothetica* holotype female from Florida, USA. Scale = 1 mm

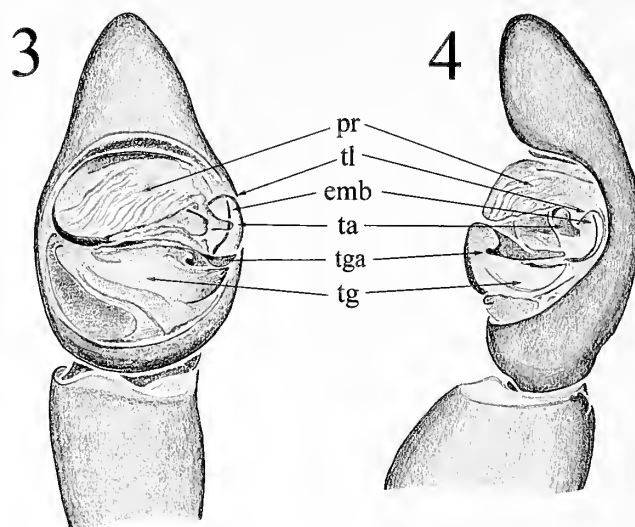
8♀, H.K. Wallace (FSCA). *Mississippi*: 1♂2♀ Hancock County, 42 mi East of New Orleans, 30°18'N, 089°20'W, 15 July 1939, H.K. Wallace (FSCA).

Other material examined.—USA: *Alabama*: 2♀ Baldwin County: Foley, 30°24'N, 087°41'W, 25 June 1912 (FSCA). *Florida*: 1♀ Alachua County, 29°39'N, 082°19'W, 26 January 1958, H.V. Weems Jr. (FSCA).

Etymology.—Wallace did not comment on etymology. However, *apothetica* is presumably derived from a Greek word meaning storehouse, and could refer to the Devil's Mill Hopper near the type collection locality (Dondale, pers. comm. 2007).

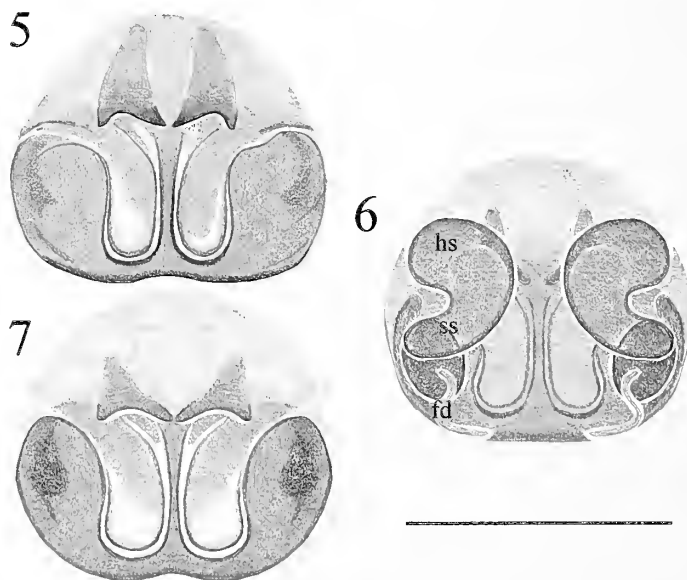
Diagnosis.—Males of *V. apothetica* are distinguished from other members of this genus by the large palea, which lacks sclerotization, a transparent terminal apophysis superior to the tegular lobe, and the relatively small tegular apophysis (Figs. 3, 4). Females are separated from their congeners by the anteriorly widened curved portion of the transverse piece of the median septum, each being about one-third the width of the entire epigynum (Figs. 5, 7).

Description.—*Male*: Chelicerae: light tan; without strong boss; three promarginal and retromarginal teeth. Carapace (Fig. 1): light yellow background with medium brown markings; median light stripe extending from between eyes to rear of carapace containing two darkened areas posterior to PLEs; submarginal light bands; wavy dark margins; few dark brown radial lines running from median light area to submarginal light area; darkened region surrounding ALEs and PER; AER slightly procurved; eyes and anterior portion



Figures 3, 4.—*Varacosa apothetica* allotype male from Alachua County, Florida, USA: 3. Ventral aspect of palp; 4. Retrolateral aspect of same. pr = palea region; tl = tegular lobe; emb = embolus; ta = terminal apophysis; tga = tegular apophysis; tg = tegulum. Scale = 1 mm

of carapace lightly iridescent. Dorsum of abdomen: light yellow background, uniformly mottled medium grey; heart mark may be present, if so not strongly outlined; weak chevrons if any; darker anteriorly. Legs: femora annulate; ventral surface of femur iridescent, perhaps even the entire leg; leg formula IV:I:II:III. Endites and labium: light yellow overall, darker proximally; labium nearly square. Sternum: yellow; bare but for disparate long setae. Venter: yellow; low numbers of small dark spots near the margins. Pedipalpus (Figs. 3, 4): large, wrinkled palea; tegular apophysis with strong sclerotization on dorsal tip; slightly curved embolus lying in distally elongated tegular lobe; transparent terminal



Figures 5-7.—5. Ventral aspect of epigynum, *Lycosa apothetica*, holotype female from Alachua County, Florida, USA. 6, 7. *Varacosa apothetica* paratype female from Alachua County, Florida, USA: 6. Internal genitalia; 7. Epigynum of same. hs = head of spermathecae; ss = stalk of spermathecae; fd = fertilization ducts. Scale = 0.5 mm



Figure 8.—Map of *Varacosa apothetica* collection locality records, Southeastern United States. Scale = 150 mi/240 km

apophysis protruding from palea over the conductor and embolus when viewed dorsally; tegulum devoid of major topography or scleritization; no macrosetae on tip.

Female: similar to male. Carapace (Fig. 2); Epigynum (Figs. 5, 7): Thin median septum; thin transverse piece, except for heavily thickened anterior lobes, each nearly one-third the width of the epigynum; deep excavations along margin of median septum and transverse piece; median septum and transverse piece sclerotized; hoods triangular; whole of epigynum nearly circular. Spermathecae (Fig. 6): Large spermathecae extending anteriorly from lateral position; stalk of spermathecae angled toward top of median septum before bending $> 90^\circ$ and widening into head of spermathecae; fertilization ducts appear suspended above darkened structure posterior to spermathecae when viewed from within.

Measurements.—Wallace's original measurements (1947) for both the male and female are again reported here in Table 1.

Distribution and habitat preferences.—Wallace's records (1947) indicate that this species is found only in the southeastern USA, from Florida and Georgia west to Mississippi (Figure 8). Most specimens have been collected in Gainesville, Florida. Wallace (1947) reports that "Males have been collected only in October, November, December, and February while females have not been taken after May until October." It is "secretive," "usually stays close by, or in, the mouth of it's [sic] retreat" and is "usually found in moist situations in pine flatwoods (pond margins, cypress bay margins, etc.), but may be found occasionally in other situation [sic]" (Wallace 1947).

Remarks.—Wallace (1947) lists 57 paratypes in his original description. I examined the majority of those, and three additional specimens collected later. This species bears a synapomorphy with *Varacosa*: the conspicuous anterior curvatures of the transverse piece. I therefore support Roewer's combination: *Varacosa apothetica* (Wallace 1947), contra Platnick (2008). In *V. apothetica* these structures are much wider than those of other *Varacosa*. Of its congeners, the *V. apothetica* epigynum most closely resemble *V. gosiuta* (Chamberlin 1908) and *V. shenandoa* (Chamberlin & Ivie 1942) (Brady 1980). The palp of the male differs from most

Table 1.—Features of *V. apothetica* (Wallace), taken from Wallace (1947). All measurements in millimeters. See text for abbreviations.

Dimension	<i>V. apothetica</i> ♂	<i>V. apothetica</i> ♀
CW	2.5	2.9
CL	3.5	4.0
POQW	1.0	1.4
POQL	0.8	1.0
PMEW	0.4	0.4
PLEW	0.3	0.3
CH	0.6	0.6
PF	1.3	1.4
PP	0.6	0.7
PT	0.6	0.8
PC/PTC	1.0	1.2
F1	2.7	3.9
P1	1.4	1.5
T1	2.3	2.2
M1	2.3	2.0
T1	1.5	1.5
Total 1	10.2	11.1
F2	2.4	2.7
P2	1.3	1.5
T2	2.0	2.0
M2	2.1	2.0
T2	1.5	1.5
Total 2	9.3	9.7
F3	2.4	2.6
P3	1.2	1.3
T3	1.7	1.8
M3	2.3	2.2
T3	1.3	1.5
Total 3	8.9	9.4
F4	3.1	3.3
P4	1.2	1.6
T4	2.5	2.8
M4	3.3	3.7
T4	1.8	1.9
Total 4	11.9	13.3

other *Varacosa*, featuring a large palea and relatively small median apophysis similar to that of *V. hoffmannae* Jiménez & Dondale 1988.

One notable feature of this species is the iridescent quality noted on the body of the males. Male specimens exhibited varying levels of iridescence over their bodies, but each was found to have femora that bore this quality. It is not clear if this is an artifact of the long term preservation of these specimens or a true characteristic of the species.

ACKNOWLEDGMENTS

I wish to thank the following individuals for their contribution to this work Allen R. Brady and Charles D. Dondale for their identification of this project and helpful encouragement; Norman I. Platnick (AMNH) and G.B. Edwards (FSCA) for the loan of specimens; Lou Sorkin (AMNH) for his assistance with material; C.D. Dondale and Thomas L. Bultman for reading an early version of the manuscript; Dr. Volker Framenau, an anonymous reviewer, and Dr. Ingi Agnarsson for their helpful critiques during the review process; Sarah C. Crews for her suggestions in relation to the illustrations; and the Hope College Department of

Biology, particularly the Chair T.L. Bultman, for support of this research.

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Description of *Zabius gaucho* (Scorpiones, Buthidae), a new species from southern Brazil, with an update about the generic diagnosis

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Abstract. This paper provides the description of a new species in the genus *Zabius* Thorell (Scorpiones, Buthidae), *Z. gaucho* n. sp., from four localities in the State of Rio Grande do Sul, Brazil. It differs from *Zabius fuscus* (Thorell 1877) and *Z. birabeni* Mello-Leitão 1938 in details of the telson shape, the longitudinal carinae on mesosomal tergites II–VI, and the number of pectinal teeth. The genus was hitherto known only from Argentina, *Z. fuscus* being a frequent inhabitant of the central Sierras; *Z. birabeni*, in turn, is probably a rare and non-orophilous scorpion, collected in scattered localities on the monte/chaco ecotone and in northern Patagonia. The presence of a species of *Zabius* in southern Brazil lends additional support to the generalized distributional track known as “peripampasic track,” which zoogeographically links the central Sierras Pampeanas with ancient mountains in the southern province of Buenos Aires, southeastern Uruguay and southern Brazil.

Keywords: Scorpions, Neotropics, Argentina, taxonomy, new records

Resumo. Neste trabalho descrevemos uma espécie nova do gênero *Zabius* Thorell (Scorpiones, Buthidae), *Z. gaucho* n.sp., procedente de quatro localidades do Rio Grande do Sul, Brasil. Distingue-se de *Zabius fuscus* (Thorell 1877) e *Z. birabeni* Mello-Leitão 1938 por detalhes da morfologia do telson, das cristas longitudinais dos tergitos do mesossoma, e pelo número de dentes pectíneos. O gênero era conhecido até o momento só para a Argentina, sendo *Z. fuscus* um escorpião muito freqüente na região serrana central; *Z. birabeni*, no entanto, é aparentemente uma espécie não orófila e rara, coletada em localidades dispersas no ecótono monte/chaco (oeste do país) e no norte da Patagonia. A presença de uma espécie de *Zabius* no sul do Brasil representa um apoio adicional ao padrão generalizado de distribuição denominado de “track peripampasico”, que vincula zoogeograficamente as Sierras Pampeanas com sistemas orográficos antigos do sul da Província de Buenos Aires, do sudeste do Uruguai e do sul do Brasil.

The small buthid genus *Zabius* Thorell 1894 is restricted to Argentina and previously included only two nominal species: *Z. fuscus* (Thorell 1877) and *Z. birabeni* Mello-Leitão 1938. The former species is a very common scorpion occurring in orographic systems in central Argentina, while the latter seems to be a rare species, reported from scattered rockless localities in western and northern Patagonia (Abalos 1953; Maury 1979; Acosta 1989, 1993, 1996; Acosta & Rosso de Ferradás 1996; Mattoni & Acosta 1997; Acosta & Maury 1998; Ojanguren Affilastro 2005). Therefore, the discovery of several specimens of a hitherto undescribed species of *Zabius* in the State of Rio Grande do Sul, Brazil, represents a remarkable novelty. This new species is described below as *Zabius gaucho* n. sp. In this paper we also provide new records for *Z. fuscus* and *Z. birabeni* and discuss some doubtful reports of the former. Abbreviated synonymies are given to include a few references overlooked by or published after Fet & Lowe (2000). Since the generic diagnosis of *Zabius* available in the literature is brief (e.g., Mello-Leitão 1945; Abalos 1953), we provide a more complete version, both so as to cover the character states peculiar to *Z. gaucho* n. sp. and to include several characters introduced by recent taxonomists. *Zabius* is the southernmost

buthid genus occurring in South America and also worldwide. The Neotropical region contains relatively few genera of that family, although one of them, *Tityus* C.L. Koch 1836, is the most speciose in the order (Fet & Lowe 2000). The presence of a member of *Zabius* in the state of Rio Grande do Sul has interesting biogeographic implications since it adds further evidence supporting the extension of the generalized distributional track known as the “peripampasic track” (Acosta 1989, 1993) into southern Brazil as briefly discussed below.

METHODS

Descriptions and line drawings were made using a Leica MS5 stereomicroscope equipped with drawing tube. Measurements were taken with a graduated ocular and followed guidelines of Stahnke (1970). Photographs were made using a Canon 400D XTi with a 100 mm Macro-Canon lens. Descriptive terms and abbreviations are as follows: carapacial carinae (Stahnke 1970): AM, anterior median; CM, central median; PM, posterior median; CL, central lateral. Carapacial furrows: based on Stahnke (1970), not abbreviated. Mesosomal carinae (adapted from Vachon 1952): MD, median; SM, submedian; SL, sublateral. Carinae of metasomal segments (Francke 1977). Segments I–

IV: DL, dorsal lateral; LSM, lateral supramedian; LIM, lateral inframedian; VL, ventral lateral; VSM, ventral submedian. Segment V: DL, dorsal lateral; LM, lateral median; VL, ventral lateral; VSM, ventral submedian; VM, ventral median. Chelal carinae (Soleglad & Sissom 2001; partially also Vachon 1952): D1, digital; D3, dorsal secondary; D4, dorsal marginal; D5, dorsal internal; I, internomedian; V3, ventrointernal; V1, ventroexternal; E, external secondary; VA, ventral accessory. Carinae on pedipalp femur and patella are given topological terms, to replace the use of "internal" and "external" (actually, structures inside or outside the tegument); correspondences with Stahnke's (1970) nomenclature in brackets: prodorsal (instead of dorso-interior), retrodorsal (dorso-exterior), proventral (ventro-interior), retroventral (ventro-exterior), dorsal median (dorso-median), ventral median (ventro-median), retrolateral median (exterior-median), prolateral median (not mentioned in Stahnke 1970).

Acronyms of repositories.—CDA: Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina; IBSP: Instituto Butantan, São Paulo, Brazil; LEA: Collection of Luis E. Acosta, Córdoba, Argentina; MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MCN: Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MNRJ: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; ZMH: Zoologisches Museum, Hamburg, Germany.

Additional material examined.—*Tityus argentinus*: ARGENTINA: *Jujuy*: Parque Nacional Calilegua, Toma de Agua (1340 m), 23°41'S, 64°52'W, 25 February 1997 (L. Acosta), 1 ♂ (LEA). *Tityus bahiensis*: BRAZIL: *Mato Grosso do Sul*: Brasilândia, Fazenda Barma, 21°15'S, 52°03'W, 20 February 1993 (A.F. Beck, J.O. Silva), 1 ♂, 1 ♀ (LEA). *Tityus confluens*: ARGENTINA: *Córdoba*: Chancaní, 31°22'S, 65°29'W, 19 December 1987 (L. Acosta, F. Pereyra), 4 ♀ (CDA 000.506). *Tityus fasciolatus*: BRAZIL: *Distrito Federal*: Brasília, 15°48'S, 47°55'W, April 1992 (M. Knox Brito), 1 ♂, 1 ♀ (LEA). *Tityus serrulatus*: BRAZIL: *Distrito Federal*: Brasília, 15°48'S, 47°55'W, April 1992 (M. Knox Brito), 1 ♀ (LEA). *Tityus trivittatus*: ARGENTINA: *Santa Fe*: Santa Fe, 31°38'S, 60°42'W, January 1985 (C. Espíndola), 1 ♀ (CDA 000.533). *Tityus uruguayensis*: URUGUAY: *Canelones*: 1 ♂, Solymar Norte, 34°49'S, 55°56'W, 18 February 1999, C.A. Toscano-Gadea (LEA). *Centruroides sculpturatus*: USA: *Arizona*: 5 specimens, Alamo Dam State Park, Yuma Co., 34°14'N 113°35'W, 1 May 1970, M.A. Cazier (LEA). *Rhopahurus aganemnon*: BRAZIL: *Goiás*: 3 specimens, Campinaçu, Serra da Mesa, ca. 13°51'S, 48°33'W, 18 February–2 March 1996, Silvestre, Brandão, Yamamoto (LEA). *Rhopahurus rochae*: BRAZIL: *Bahia*: 2 specimens, Caatinga do Moura, 10°59'S, 40°45'W, 24–29 January 1980, P.E. Vanzolini (LEA).

SYSTEMATICS

Family Buthidae C.L. Koch 1837

Genus *Zabius* Thorell 1894

Zabius Thorell 1894:279.

Type species.—*Isometrus fuscus* Thorell 1877 by original designation.

Diagnosis.—Small to medium-sized scorpions (up to 65 mm). General color yellowish to dark ferruginous, tegumentary carinae usually darker. Anterior margin of carapace with a notch; ocular mound slightly displaced anteromedially. Most carapacial carinae not easily recognizable, normally obscured by the irregular granulation: AM and CM feeble or absent, PM fairly or well developed between the slight transverse posterior furrow and the posterior border. Sternum narrowed elongated pentagonal, Type 1 (nomenclature after Soleglad & Fet 2003): apex reduced and slightly depressed, bordered posteriorly by well defined lobes (resembling the anterior part of the lateral lobes of Type 2 and giving the sternum the appearance of being anteriorly bifid); posterior depression very deep, not surrounded by lobes. Mesosomal tergites I–VI with three distinct longitudinal carinae (one MD, two SM), tergite VII with five carinae. Sternite V with two SM and two SL carinae. Metasoma slender. Metasomal segments I–III bearing ten longitudinal carinae (LIM complete in segment I, but much weaker or almost vanishing in segments II and III); segment IV with eight carinae (LIM lacking); segment V with five carinae (complete), plus VSM carinae limited to the proximal half. Telson without subaculear apophysis; a blunt small protuberance is present instead; vesicle globose (*Z. fuscus*, *Z. birabeni*) or more elongated (*Z. gaucho* n. sp.), aculeus relatively short. Pedipalp chela dilated, with a lobe at the base of the movable finger, corresponding to a notch in the fixed finger (both dilatation and lobation more accentuated in males). Nine chelal carinae (Figs. 10–12, 14), eight being complete, plus a short basal VA between E and V1, separating trichobothria *Eb*₁ and *Eb*₂ (Abalos 1953: 350 named this shortened VA the "dorsal accessory"); angle D3:D4:D5 \cong 90°. Chelal carinae are conspicuous and well defined, except for V3, the granulation (or crenulation) of which is present only in the basal third, the rest being a smooth tegumentary border. Denticular margin of the movable finger with 9–12 oblique rows, with outer and inner accessory denticles, but without supernumerary denticles. Trichobothriotaxy: subtractive neo-bothriotaxy, type A, group α (Vachon 1974, 1975); femur with 10 trichobothria (*d*₂ missing), patella with 13 (*d*₂ very small and difficult to see), chela with 15. Pectines with fulcrum. Legs without tibial spur; prolateral basitarsal spur on legs III and IV bifid.

Comments on chelal carination.—The number and nomenclature of carinae on the chela received some attention in the literature. Vachon (1952) recognized a maximum of seven chelal carinae, while Stockwell (1989) proposed a pattern of eight basic carinae. More recently Prendini (2000), followed by Soleglad & Sissom (2001), identified a derived pattern of 10 carinae in most non-buthids, whereas buthids (represented as out-group in their analyses only by the genus *Centruroides* Marx 1890) were characterized as having an eight-carinate condition, presumably basal for the order. There are many genera of Buthidae without or with very obsolete chelal carinae, so that a homology assessment is difficult. Others (e.g., *Zabius* and examples mentioned below) have, in contrast, well developed carinae suggesting that a 9-carinae pattern might be the basic condition for this family. In their character state statement Prendini (2000) and Soleglad & Sissom (2001) overlooked an "accessory" carina (VA), feeble in some *Centruroides* but well developed in several other buthids. In *Zabius*, carination is strong, and nine carinae can clearly be identified (Figs. 10–12, 14) as described by Abalos (1953) and

Ojanguren Affilastro (2005). Assuming that D2 (subdigital) and V2 (ventral median) are lacking, and using D1 (digital) and V1 (ventral external) as "landmarks" an additional short though well defined carina (VA, ventral accessory; Vachon 1952) is observed between V1 and E. *Trichobothrium* Eb_3 is placed in the interearinal sector D1–E, Eb_2 between E and VA, and Eb_1 between VA and V1. The same condition (short, well defined VA, and the described arrangement of *Eb* triehobothria) was verified in *Tityus argentinus* Borelli 1899, *T. baltiensis* (Perty 1833), *T. confluent* Borelli 1899, *T. fasciolatus* Pessôa 1935, *T. serrulatus* Lutz & Mello 1922, *T. trivittatus* Kraepelin 1898 and *T. uruguayensis* Borelli 1901 (L. Acosta pers. obs.). A rapid survey of the literature revealed a similar arrangement in at least 20 additional species of *Tityus* as well as in members of *Alayotityus* Armas 1973, *Tityopsis* Armas 1974, and *Microtityus* Kjellesvig-Waering 1966 (Armas 1984; Lourenço & Vachon 1996). The development of VA appears to be somewhat variable in *Centruroides*: in *C. margaritatus* (Gervais 1841), *C. exsul* (Meise 1934), and *C. testaceus* (DeGeer 1778) it is short and granular, while in *C. gracilis* (Latreille 1804) it is obsolete (Sissom & Francke 1983; Sissom & Lourenço 1987, designated as "external secondary" therein). In *Centruroides exilicauda* (Wood 1863), the position of VA is occupied by a V-shaped rugulose sculpturation, not well defined, which leaves Eb_1 and Eb_2 to each side. VA is rudimentary (as an irregular row of small granules) in *Rhopalurus rochae* Borelli 1910 and *R. agamemnon* C.L. Koch 1839 (L. Acosta pers. obs.).

In Old World buthids, when present, VA appears to have a full extension. In two *Hottentotta* species illustrated in Lamoral (1979, figs. 45 and 66, *sub Buthotus*), a diagonal VA carina runs between Eb_2 and Eb_3 , extending along the entire palm to the articular condyle. In a generalized drawing, Vachon (1952:62, fig. 69) shows a complete VA, too. In ventral view (figs. 46 and 67 of Lamoral 1979), a longitudinal carina is observed from the same condyle up to the palm base in the position typical to V1. Further Old World buthids with a complete VA include, e.g., *Butheolus thalassinus* Simon 1882 (smooth to finely granular), *Compsobuthus acutecarinatus* (Simon 1882) (faint, smooth ridge), *C. brevimanus* (Werner 1936) (faint, granular ridge), and *Androctonus bicolor* Ehrenberg 1828 (strong, smooth) (Sissom 1994; M. Soleglad, *in litt.*), whilst the illustration of *Compsobuthus vachoni* Sissom 1994 suggests a short VA (Sissom 1994:19). Although examples are not intended to give an exhaustive revision, it seems clear that the full VA carina of Old World representatives and the shortened version in *Zabius*, *Tityus*, *Centruroides*, *Tityopsis*, and *Alayotityus* likely represent two states of the same feature. If homologies, as currently assessed, are correct (especially concerning the identification of V1), VA might prove to be unique for buthids, not found elsewhere in the order.

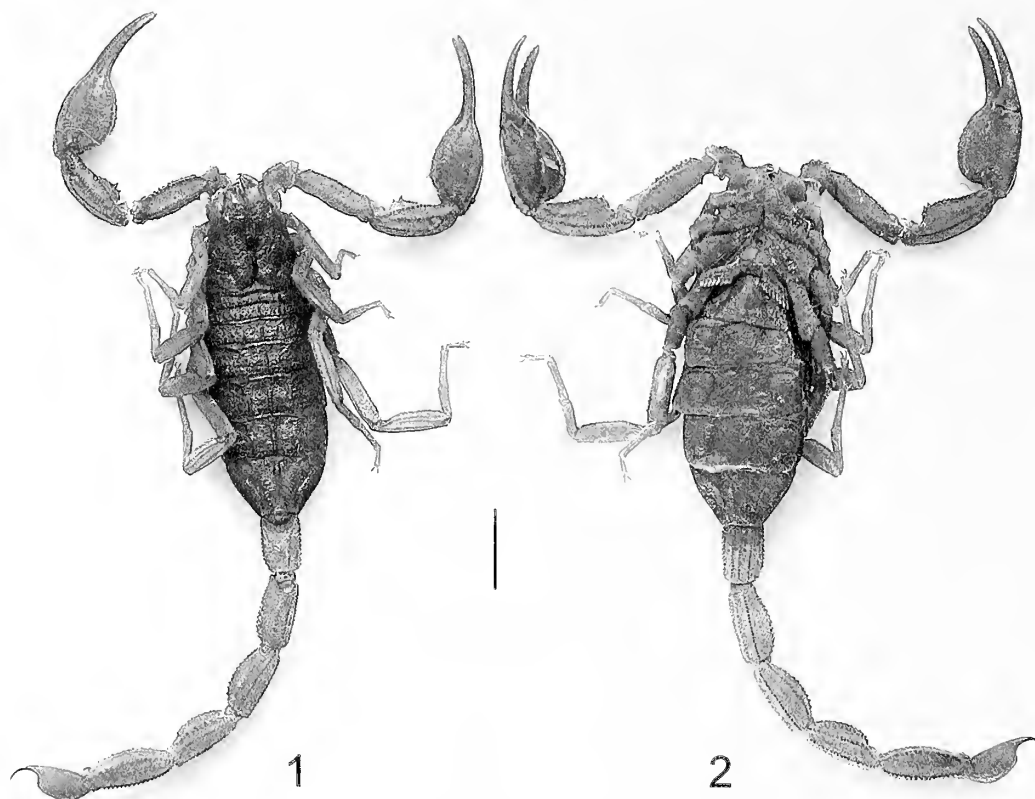
Included species.—*Zabius fuscus*, *Zabius birabeni*, and *Zabius gauchus* new species.

Distribution.—South America: Central Argentina to northern Patagonia; southern Brazil (Fig. 15); Paraguay? The presence of a *Zabius* species in southern Brazil adds evidence to the so called "peripampasic track" (Acosta 1989, 1993). This generalized track was identified through the approximate congruence of the distributions of several scorpion and opilionid taxa, primarily connecting the Pampean Sierras in central Argentina (provinces of Córdoba and San Luis), with low systems in the province of Buenos Aires (Tandilia and Ventania), and in southeastern

Uruguay. Additional extensions of the track were suggested both to sub Andean chains in northwestern Argentina, and to southern Brazil (Acosta 1989, 1993). Scorpion taxa which support this distributional pattern are: (1) the *Bothriurus* *prospicius* species group, ranging from northwestern Argentina to Uruguay (Acosta & Peretti 1998), with a hitherto unnamed species in southern Brazil (C. Mattoni pers. comm.), (2) the *Bothriurus* *flavidus* species group, with one widespread species occurring in Córdoba, San Luis, La Pampa and Buenos Aires, and one undescribed species in Uruguay (L. Acosta & C. Toscano-Gadea unpubl.), (3) the *Urophonius* *brachycentrus* species group, with one species widely distributed in central Argentina, and a second in the province of Buenos Aires, Uruguay, and southern Brazil (Maury 1977). The recent discovery of new species either in Uruguay or Brazil (*Z. gauchus* and the above mentioned *Bothriurus*) was indeed at least predictable based on the track pattern. While the track is presumed to link old mountains, most scorpions in it are no longer strictly orophilous, although their distributions appear to be primarily associated with those ranges. Harvestmen of the peripampasic track include: (a) representatives of the genus *Ceratontia* Roewer 1914 (Triaenonychidae), with one species in the central sierras + Ventania, another one in Tandilia + Ventania + Uruguayan ranges + southern Brazil, and a third one in southern Brazil (Maury & Roig Alsina 1985; Maury 2000), and (b) genus *Neopucroliella* Roewer 1931 (Gonyleptidae), with several species in the central sierras and one in Ventania (this is the only taxon not yet recorded in Uruguay or Brazil; Acosta 1990).

KEY TO THE SPECIES OF *ZABIUS*

1. Mesosomal tergites II–VI: SM carinae extended posteriorly in a noticeable projection (at least with the length equivalent to three granules; Fig. 13); anterior margin of carapace with a moderate notch (Figs. 3, 4); pectines with 7–10 teeth (female, male unknown); pectinal basal plate subrectangular (Fig. 7); telson only slightly globose, somewhat elongated; subaculear tuberosity weakly developed (Fig. 5). *Z. gauchus*
2. Mesosomal tergites II–VI: SM carinae not extended posteriorly in a projection, but end at the tergite margin or with at most a single granule prominent; front border of carapace with an accentuated notch (Fig. 8); pectines with 11–15 teeth (male and female); pectinal basal plate divided in two lobes by a noticeable notch on the anterior border (Fig. 9); telson markedly globose, subaculear tuberosity small but evident *Z. fuscus*
2. Total length up to 65 mm. General color dark ferruginous to light hazel. Stigmata elliptical; metasomal segment V: VL carinae uniformly granular, ranging from a row of small granules to small blunt tubercles, none of which is noticeably larger than the rest; denticular margin of the movable finger of the pedipalp chela with 12 oblique granular rows *Z. birabeni*
- Total length up to 45 mm; general color straw yellow; stigmata rounded; metasomal segment V: VL carinae with 2 or 3 large, tall tubercles or small apophyses in the middle, which are clearly distinct from the remaining granules in the row; denticular margin of the movable finger of the pedipalp chela with 9 or 10 oblique granular rows *Z. birabeni*



Figures 1, 2.—*Zabijs gaucho* new species, female paratype (Riozinho, IBSP). 1, Dorsal aspect. 2. Ventral aspect. Scale line: 5 mm.

Zabijs gaucho new species

Figs. 1–7, 10–13

Type material.—BRAZIL: *Rio Grande do Sul*: holotype female, Taquara, Morro do Itacolomi (29°38'S, 50°46'W), 16 July 1992, L. Frug (MCN 553). Paratypes: BRAZIL: *Rio Grande do Sul*: 1 female, Nova Petrópolis (29°21'S, 51°08'W), 4 August 1993, E.E. Ely (MCN 580); 1 female, Riozinho (29°38'S, 50°27'W), 21 January 2002, A.D. Brescovit (CDA 000.254); 1 female, same locality, 17 December 2001, I. Bernard (IBSP 3464); 1 female, “Taguara del Mondo nuovo” [actually Taquara], Mus. Straßburg, c. 1893 (c. = exchanged), det. “*Tityus*—(*Phaesus*) [*Zabijs*] *fuscus*” [stricken out and corrected on the label] (ZMH).

Other material examined.—BRAZIL: *Rio Grande do Sul*: 1 ♀, Tenente Portela (27°22'S, 53°46'W), 17 December 2002, M. Dorneles (MCN 720, damaged).

Etymology.—The species name is derived from the Portuguese adjective “gaucho,” treated here as indeclinable; it is popularly applied to the inhabitants of the Brazilian state of Rio Grande do Sul, where the new species was collected.

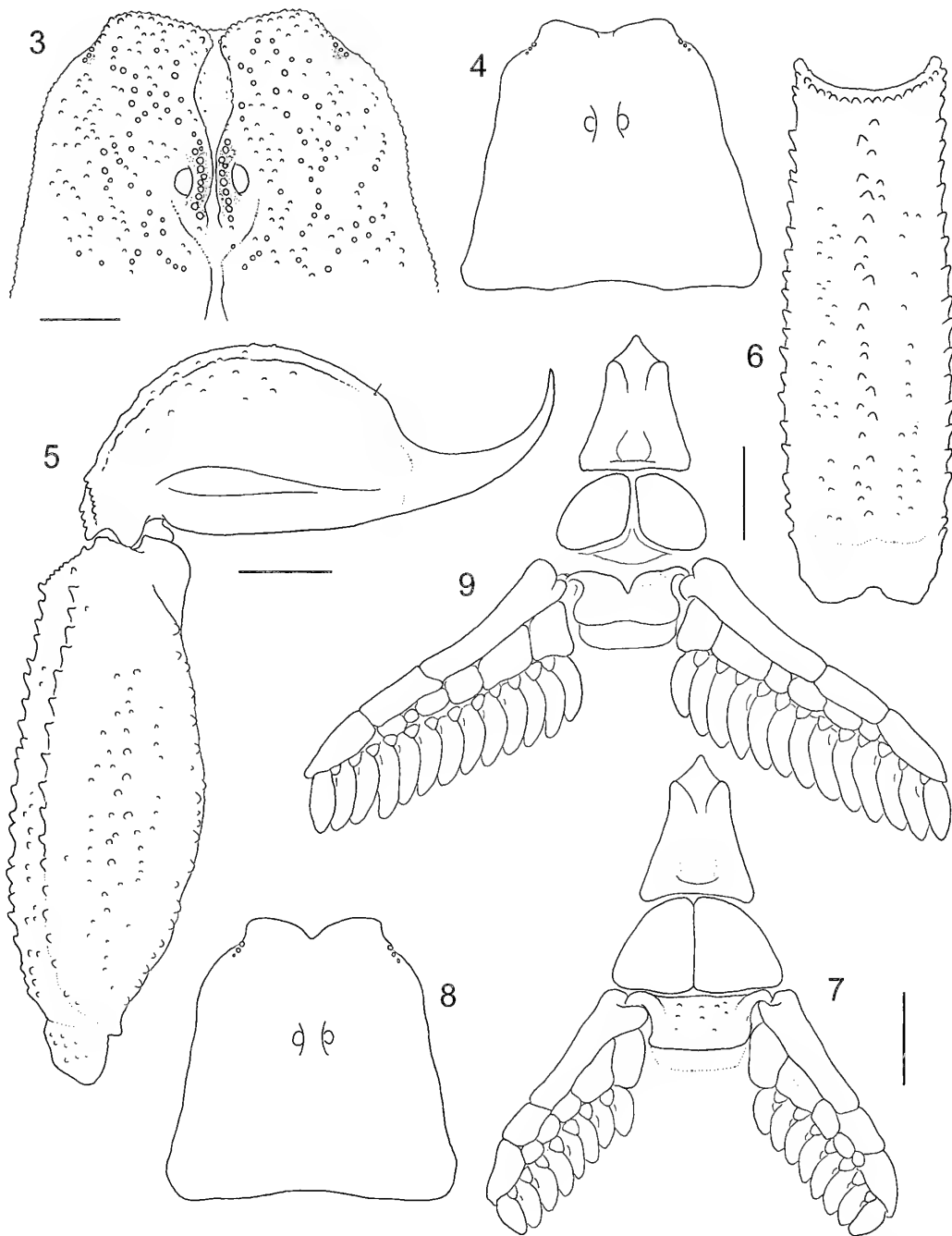
Diagnosis.—Mesosomal tergites II–VI with SM carinae extended in a short but conspicuous posterior projection. Anterior margin of carapace with a moderate notch. Pectines with 7–10 teeth; basal plate subrectangular. Telson only slightly globose, somewhat elongated; subaculear tuberosity little developed. Because of their similar size and coloration (hazel to dark ferruginous), the overall appearance of *Z. gaucho* n. sp. resembles that of *Z. fuscus* (*Z. birabeni* is readily separated because of its small size, its lighter coloration, and the distinctive small apophyses on VL carinae of metasomal segment V). A careful examination reveals, however, that *Z.*

fuscus shares more diagnostic characters with *Z. birabeni* than with *Z. gaucho* n. sp. In both *Z. fuscus* and *Z. birabeni* the carinae of mesosomal tergites do not show marked projections and the telson is more markedly globular (cf. Ojanguren Affilastro 2005). They also have higher pectinal teeth counts, and the pectinal basal plate has a distinctive anterior notch as if composed of two halves fused medially (Fig. 9). Specimens of *Z. gaucho* n. sp. show a faint and irregular reticulate pigment, especially on the mesosomal tergites, which is not present in the congeners. Granules of some carinae or granular areas (e.g., medial border of pedipalp femur; DL carinae all along the metasoma) are taller and more acute in *Z. gaucho* n. sp. Carapace carinae are poorly defined in all three species, even least defined in the new species.

Description.—Male unknown. Females: total body length 41.7–55.3 mm. Detailed measurements of holotype, together with summary values of the available sample (mean, maximum, minimum): Table 1.

Color. General color reddish hazel, with granules and pedipalp fingers darker; legs and ventral side (coxae, sternal region, pectines, sternites I–III) lighter, sternites IV and V gradually darkening to the general coloration; chelicerae yellowish, with reticulate pigment dorsally on the cheliceral hand behind the fingers. Carapace and especially mesosomal tergites with very faint reticulate pigmentation.

Morphology. Carapace anterior margin with a V-shaped but not accentuated median notch, bordered by a granular row. Surface of carapace covered by coarse granulation. Median anterior and median central furrows shallow, the former wider; median posterior and postmarginal furrows forming a deep triangular depression. Lateral posterior furrow deep, the

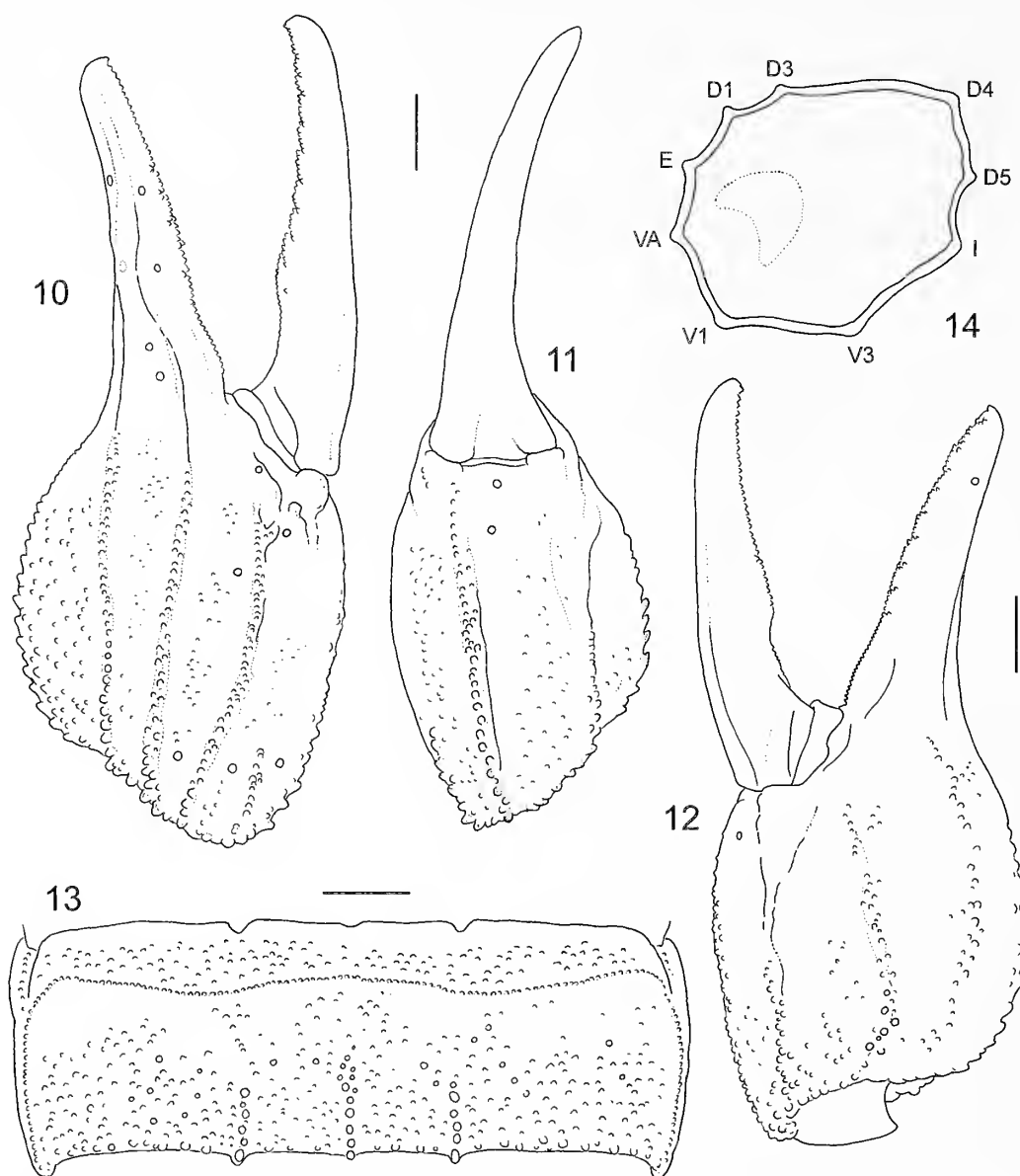


Figures 3–9.—*ZabiUS* species. 3–7. *Z. gauchO* new species. 3. Carapace, front half. 4. Outline of carapace. 5. Telson and metasomal segment V, lateral view. 6. Metasomal segment V, ventral view. 7. Sternum, genital operculi, pectinal plate and pectines. 8, 9. *Z. fuscus* (Thorell). 8. Outline of carapace. 9. Sternum, genital operculi, pectinal plate and pectines. Scales: 1 mm (Figs. 4 and 8 not at scale).

remaining ones just insinuated by a slight depression and/or lack of granulation. Most carapacial carinae unrecognizable, much less defined than in congeners, AM and CM almost absent; short superciliary crest as a row of pearl-like, dark conspicuous granules, leaving a well defined interocular groove in between; CL represented by an oblique row of small granules (most granulation on the area is oriented a similar way); PM fairly defined along the longitudinal tegumentary ridge each side of the posterior marginal furrow, up to the posterior transverse furrow. Posterior margin with a row of granules; posterior end of PM terminates with a pointed

granule on the carapace margin, aligned with the SM carinae of tergites (see below).

Mesosomal tergites: finely granular on the pretergites and the anterior half of tergites, the posterior half with coarse granulation, as on carapace. Tergites I–VI with three aligned longitudinal carinae (one MD, two SM). MD very short on tergite I, becoming more developed posteriorly (on tergite II it is extended up to one third of the tergal plate, III and IV up to the half, and almost complete on V and VI); in all cases ending in a blunt granule. SM carinae shorter than MD; they are feeble on tergite I, but on tergites II–VI ending in an acute granule of



Figures 10–14.—*Zabius* species. 10–13. *Z. gaucho* new species. 10–12. Right pedipalp chela: 10. Lateral view, 11. Ventral view, 12. Mesal view. 13. Mesosomal tergite V, dorsal view. 14. *Z. fuscus* (Thorell), schematic transverse section of the right pedipalp chela (basal third), showing all nine carinae. Abbreviations: D1, digital, D3, dorsal secondary, D4, dorsal marginal, D5, dorsal internal, I, internomedian, V3, ventrointernal, V1, ventroexternal, E, external secondary, VA, ventral accessory. Scales: 1 mm (Fig. 14 not at scale).

increasing size, almost resembling a tiny apophysis over the tergite's edge. Tergite VII with SL and SM carinae complete, MD restricted to a very short, basal portion. Sternites I and II almost smooth, from sternite III onwards, coarsely granular on the lateral border, and SL carinae insinuated; these are more defined on sternite IV; sternite V granular, SM and SL carinae almost complete (they do not reach the anterior border). Stigmata oval. Number of pectinal teeth ($n = 11$): 7 teeth (2 pectines), 8 (8), 10 (1); holotype with 10-[damaged].

Metasoma. Segments I–IV: VSM, VL, LSM, and DL carinae complete, the latter with large and acute granules (especially posteriorly); LIM complete on segment I, it is very weak on segments II and III, and is absent on segment IV. Segment V: VM and VL complete, VSM less conspicuous and restricted to the basal half; LM is represented by few unordered granules, while DL are complete but little evident, formed by blunt

granules. Telson slightly globose, with almost no trace of subaculear tubercle; ventral surface rugulose. Pedipalps. Medial surface of trochanters coarsely granular, granules are especially tall and acute proventrally. Pro- and retrodorsal and proventral carinae of femur complete, regularly granular; prolateral median carina of tall conical, unequal granules or small apophyses; retrolateral median carina homogeneously crenulate, ending in an acute conical apophysis near the base; retroventral carina not defined, replaced by a flattened area with subtle granulation. Patella with pro- and retrodorsal, and retroventral carinae regularly granular; proventral carina crenulate, ending in a large conic protuberance (absent on the basal third of the segment, where a smooth concavity exists); dorsal median and retrolateral median carinae feeble, ventral median very weak; prolateral surface smooth, except for a large conical protuberance, aligned with the proventral

Table 1.—Detailed measurements (mm) of the holotype female of *Zabius gauchus* n. sp. (MCN 553), and summary values for the available sample ($n = 5$; ZMH not included).

Character	Holotype	Mean (max–min)
Body length	55.3	46.5 (55.3–41.7)
Carapace length	6.6	5.7 (6.6–5.3)
anterior width	3.1	3.6 (4.1–3.0)
posterior width	6.3	6.0 (6.5–5.6)
Mesosoma length	16.6	12.5 (16.6–10.4)
Metasoma length	26.4	23.2 (26.4–20.2)
Metasomal segment I length	4.5	3.7 (4.5–3.1)
width	2.8	2.4 (2.8–2.0)
Metasomal segment II length	5.1	4.5 (5.1–3.8)
width	2.5	2.1 (2.5–1.8)
Metasomal segment III length	5.3	4.6 (5.3–4.0)
width	2.3	2.0 (2.3–1.6)
Metasomal segment IV length	5.2	4.8 (5.2–4.3)
width	2.2	1.9 (2.2–1.7)
Metasomal segment V length	6.3	5.5 (6.3–5.0)
width	2.0	1.8 (2.0–1.7)
height	2.3	2.0 (2.3–1.8)
Telson length	5.7	5.1 (5.7–4.7)
width	2.1	1.8 (2.1–1.6)
height	2.1	1.9 (2.1–1.8)
Aculeus length	2.4	1.9 (2.4–1.7)
Pedipalp total length	24.4	22.1 (24.4–20.8)
Pedipalp femur length	6.3	5.7 (6.3–5.1)
width	2.1	1.8 (2.1–1.5)
Pedipalp patella length	6.7	5.9 (6.7–5.5)
width	2.3	2.2 (2.3–2.1)
Pedipalp chela length	11.4	10.6 (11.4–10.1)
width	4.3	4.0 (4.3–3.0)
height	3.5	3.0 (3.6–2.1)
Movable finger length	7.0	6.5 (7.0–6.2)

one. Chelal earinae D1, D3, and D4 long, attaining the finger dorsum, with blunt granules on the hand but smooth on the finger; D5 and I crenulate, the area in between as a conspicuous longitudinal concavity; V1 well defined, with conspicuous granulation in all its length; V3 only granular at its base, the rest is at most a smooth weak tegumentary border; E extended up to the vicinity of the small *Esb*, it is crenulated basally, the rest with normal granulation; *V_A* carina between E and V1 crenulated, limited to the basal fourth of the manus. Trichobothriotaxy as for the genus. Denticular margin of the movable finger with 11 or 12 oblique slightly imbricate rows of granules, the most basal continued longitudinally along the edge, 11 or 12 inner and outer accessory denticles, without supernumerary granules.

Distribution.—This species has only been recorded from the state of Rio Grande do Sul, Brazil. Nothing is known about the natural history of this species. The two specimens from Riozinho were collected in urban areas, despite the fact that this city is the third best protected Atlantic Forest area, with 90% of the native forest preserved (SOS Mata Atlântica, 2004). Both specimens were collected in the same place, a peripheral district divided into several plots that has been inhabited for more than 10 years. The first specimen (CDA 000.254) was found inside a house, the second one (MCN 705) in the backyard between the house and the margin of a narrow stream in a grassy area with brick piles, stones, and wood. It is surprising that such a large and conspicuous species remained

undetected until now. Its presence in ancient collections (e.g., the specimen of ZMH), and the inclusion of *Zabius* in an old key of Brazilian scorpions (Ihering 1915) suggests that earlier authors knew or suspected the existence of this genus in southern Brazil, although it was never explicitly stated.

Zabius fuscus (Thorell 1877)

Figs. 8, 9, 14

Isometrus fuscus Thorell 1877:140.

Zabius fuscus: Thorell 1893:372; Ringuelet 1953:280; Abalos 1953:349, 350, figs. 1–22; Maury 1973:353, 363; Bucher & Abalos 1979:401, fig. 45; Gualdoni *et al.* 1986:87; Acosta 1989:122, figs 88–90; Corronca & Peralta 1995:121; Mattoni & Acosta 1997:72, 77; Fet & Lowe 2000:279 [complete reference list therein]; Ojanguren Affilastro 2005:103 [redescription, illustrations].

[*Zabius*] *fuscus*: Kraepelin 1895:8, 18 [mentioned as "*Tityus fuscus*" but accepting Thorell's combination].

Type material.—ARGENTINA: holotype, "Cordova", "Weijenbergh ded." deposited in Naturhistoriska Riksmuseet Stockholm (Coll. Thorell 43/22).

New records.—ARGENTINA: *Córdoba*: 1 ♀, Cerro Colorado, 30°06'S, 63°56'W, 21 February 1987, L. Acosta, A. Peretti (CDA 000.208); 2 ♂, between Cerro Colorado and Caminiaga, ca. 30°04'S, 63°59'W, 21 February 1987, L. Acosta (CDA 000.216); 1 juvenile, Deán Funes, 30°29'S, 64°16'W, 24 June 1986, L. Acosta (CDA 000.214); 1 ♀ with young on the dorsum, "La Industrial Salinera", between Lucio V. Mansilla and San José de las Salinas (under railway sleeper, border of saline), 29°54'S, 64°40'W, 19 November 1998, C. Mattoni, A. Peretti (CDA 000.221); 1 juvenile, between Cañada de Río Pinto and Todos los Santos, ca. 30°47'S, 64°17'W, 22 November 1986, L. Acosta (CDA 000.206); 2 ♂, Todos los Santos, 6 km to Ongamira, ca. 30°47'S, 64°23'W, 26 December 1987, L. Acosta, A. Peretti (CDA 000.209); 3 juveniles, Candonga, 31°05'S, 64°20'W, July 1957, E. Gibson (CDA 000.224); 2 juveniles, same collection data except July 1958 (CDA 000.225); 1 juvenile, Villa Colanchanga, Dique La Quebrada, 31°09'S, 64°21'W, 15 September 1985, L. Acosta (CDA 000.204); 1 ♂, 1 ♀, 2 juveniles, Cerro Uritorco, 30°51'S, 64°29'W, 2 May 1987, L. Acosta (CDA 000.218); 3 juveniles, La Cumbre, road to Cuchi-Corral, ca. 30°59'S, 64°34'W, March 1986, M. Cabrera (CDA 000.210); 1 ♂, Tiu Mayo, 2 km to La Cumbre, 30°58'S, 64°26'W, 3 May 1987, L. Acosta (CDA 000.220); 1 ♂, 1 juvenile, Vaquerías, 31°07'S, 64°27'W, 29 December 1985, L. Acosta (CDA 000.211); 1 juvenile, Cerro Pan de Azúcar, 31°14'S, 64°25'W, 15 April 1990, L. Acosta, A. Peretti (CDA 000.212); 1 juvenile, Villa San José, Mallín, 31°18'S, 64°34'W, 23 August 1986, L. Acosta, R. Pizzi (CDA 000.219); 1 ♂, 2 juveniles, Tanti, Cerro Blanco, 31°21'S, 64°36'W, July 1968, R. Martori (CDA 000.230); 2 juveniles, Villa del Lago, 31°24'S, 64°30'W, 10 May 1981, L. Acosta (CDA 000.229); 1 juvenile, San Antonio de Arredondo (in a house, upstairs), 31°29'S, 64°32'W, 27 January 1988, H. Getar (CDA 000.228); 1 ♀, Cuesta Blanca, 31°29'S, 64°35'W, January 1989, C. Boné (CDA 000.233); 1 ♀, El Diquecito, 31°22'S, 64°23'W, October 1970, Brigado, Puentes (CDA 000.226); 1 ♂, Villa Diquecito ("Las Bateas"), 31°21'S, 64°21'W, 24 October 1980, L. Acosta (CDA 000.202); 1 ♀, Córdoba (center of the

city), 31°24'S, 64°11'W, 28 November 2000, N. Fernandez (CDA 000.244); 1 juvenile, San Clemente, 31°43'S, 64°38'W, 23 September 1986, L. Acosta (CDA 000.222); 2 ♀, Atos Pampa, 31°59'S, 64°42'W, 16 December 1967, no collector (CDA 000.223); 1 ♀, between Atos Pampa and Yaeanto de Calamuchita, ca. 32°01'S, 64°42'W, 26–27 December 1987, P. Boero de Cabrera (CDA 000.203); 1 juvenile, Las Albahacas, 32°54'S, 64°50'W, 15 November 1981, M. Gualdoni (CDA 000.231); 1 ♂, 1 ♀, 3 km N of Achiras, 33°10'S, 65°00'W, 1 March 2000, L. Acosta, A. Peretti (CDA 000.026); 1 ♂, 1 juvenile, Quebrada de la Mermela, Chancaní, 31°24'S, 65°25'W, 20 December 1987, L. Acosta, F. Pereyra (CDA 000.236); 2 juveniles, Niña Paula (near Mina Clavero), 31°45'S, 64°56'W, 11 March 1981, M. Gualdoni (CDA 000.207). *San Luis*: 1 ♀, 2 juveniles, Sauce de los Chorrillos (5 km E San Luis), 33°17'S, 66°15'W, 15 July 1970, R.D. Sage (CDA 000.197); 1 ♂, 1 juvenile, 5 km road from San Francisco del Monte de Oro to Carolina, 32°40'S, 66°08'W, 12 March 1994, L. Acosta, C. Mattoni (CDA 000.199); 3 juveniles, Suyuque Nuevo, 33°08'S, 66°15'W, 14 March 1994, L. Acosta (CDA 000.200). *La Rioja*: 1 ♂, 1 juvenile, Santa Lucía, near Chamental (620–660 m), 30°29'S, 66°20'W, 6 December 1994, L. Acosta, C. Mattoni (CDA 000.085).

Distribution.—*Zabius fuscus* appears to be an almost strictly orophilous scorpion (Acosta 1989; Acosta & Rosso de Ferradás 1996) the range of which coincides with the Pampean Sierras of San Luis, Córdoba, La Rioja, Catamarca and Santiago del Estero in central Argentina (Fig. 15; Maury 1979; Acosta & Maury 1998; Ojanguren Affilastro 2005). The type locality is “Córdoba” and most likely refers to the city. Despite the statement of Teruel (2003: 147) about the “sporadic presence” of *Z. fuscus* in collections, this species is very common, and good series are available in Argentinean institutions. Many localities from Córdoba and San Luis were cited by Mello-Leitão (1934), Abalos (1953), and Ojanguren Affilastro (2005). Mattoni & Acosta (1997) added some localities in the insular sierras of the province of La Rioja (Loma Larga, between Malanzán and Loma Larga, La Calera, Olta, Dique de Olta, Quebrada del Padre), which might represent a disjunct area for the species. Specimens of *Z. fuscus* are readily caught under mid-sized or large stones. In summer, collecting with UV light suggests that many individuals hide in deep crevices of the rock walls and in “pircas” (a kind of fence made with piled stones), though not in high densities. Females are normally seen at the opening of their retreats, with only the pedipalp fingers outside, presumably to detect the presence of prey; males are more active, and more frequently are found clinging or walking on the wall. *Zabius fuscus* is commonly collected together with *Bothriurus cordubensis* Acosta 1995 and, like this species, its range excludes the higher montane belt of the Sierras Grandes (above 1800–1900 m). Aside from several findings of *Z. fuscus* in houses in small villages in the sierras, where they are thought to enter accidentally, some specimens were sporadically collected in the highly urbanized city of Córdoba (see record above), most probably because of being transported together with wood or rocks. One female with young on the dorsum was caught in an unexpected site, on the very border of the extensive saline area called “Salinas Grandes” (A. Peretti & C. Mattoni, pers. comm.). The specimen was close to an almost abandoned old salt factory under a railway sleeper

lying on a salty surface. This finding is remarkable since the site consists of a plain with only small halophilous shrubs, is surrounded by Chaco vegetation, and lies around 40 km from the nearest rocky area. Without providing details, Kraepelin (1899) recorded *Z. fuscus* from Paraguay, which was considered rather unlikely by Maury (1984) and Lourenço (1994). Kraepelin's (1899) material is stored in ZMH (“*Tityus* (~~*Phaëus*)~~ [*Zabius*] *fuscus* (Thor.), Burmeister d. 1890, Paraguay” [genus name stricken out and corrected on the label], examined). Since the specimen consists of a badly preserved juvenile and comes from a very old collection, doubts remain about the accuracy of the identification and the locality, so we agree that a further confirmation is needed. The species was also cited from the province of Jujuy (northern Argentina) by Mello-Leitão (1934) — a specimen collected by Salvador Mazza but no longer kept in any repository; Maury (1979) did not include this doubtful locality in his map. References of *Z. fuscus* from the province of Tucumán (Abalos 1953) were accepted by Maury (1979) and Corronca & Peralta (1995) but deemed to need confirmation by Mattoni & Acosta (1997) and Ojanguren Affilastro (2005). According to Teruel (2003), a specimen of *Zabius* was collected in Tucumán though the species identity remains an open question. Be this record assigned to *Z. fuscus* or not, the genus seems not as frequent in Tucumán as in other parts of its range.

Zabius birabeni Mello-Leitão 1938

Zabius birabeni Mello-Leitão 1938:84, fig. 1; Abalos 1953:353, figs. 23–27 (in part?); Fet & Lowe 2000:279 [complete reference list therein]; Ojanguren Affilastro 2005:105 [redescription, illustrations].

Type material.—ARGENTINA: *Rio Negro*: holotype male, Valcheta (40°41'S, 66°09'W), M. Birabén (Museo de La Plata 18060). According to Mello-Leitão (1938) a paratype from “Gaviotas, province of La Pampa” should exist at MNRJ, but it is not included on the type list provided by Kury & Nogueira (1999) and is probably lost.

New record.—ARGENTINA: *La Rioja*: 1 juvenile, Bajo Hondo (31°41'S, 66°00'W), 13 November 1982, E. Maury (MACN).

Distribution.—Recorded from the Argentinean provinces of Río Negro, La Pampa, Buenos Aires, Entre Ríos, La Rioja, San Juan, San Luis and Córdoba (Abalos 1953; Maury 1973; Acosta 1996; Ojanguren Affilastro 2005). With the exception of a few references from the sierras in southern province of Buenos Aires (Abalos 1953; Maury 1973; Ojanguren Affilastro 2005), whose accuracy may in some cases need revision (Acosta 1996), *Z. birabeni* is characteristic of rockless areas (Fig. 15). Although the records are somewhat scattered, most localities embrace an ample arc that roughly corresponds to an ecotonal area between Monte and Chaco+Espinal (Acosta 1996). In contrast to this wide range, the species appears to be quite rare (Acosta 1996; Ojanguren Affilastro 2005). The locality “50 km Sierra Grande”, province of Río Negro (Ojanguren Affilastro 2005), represents the southernmost record for the entire family Buthidae.

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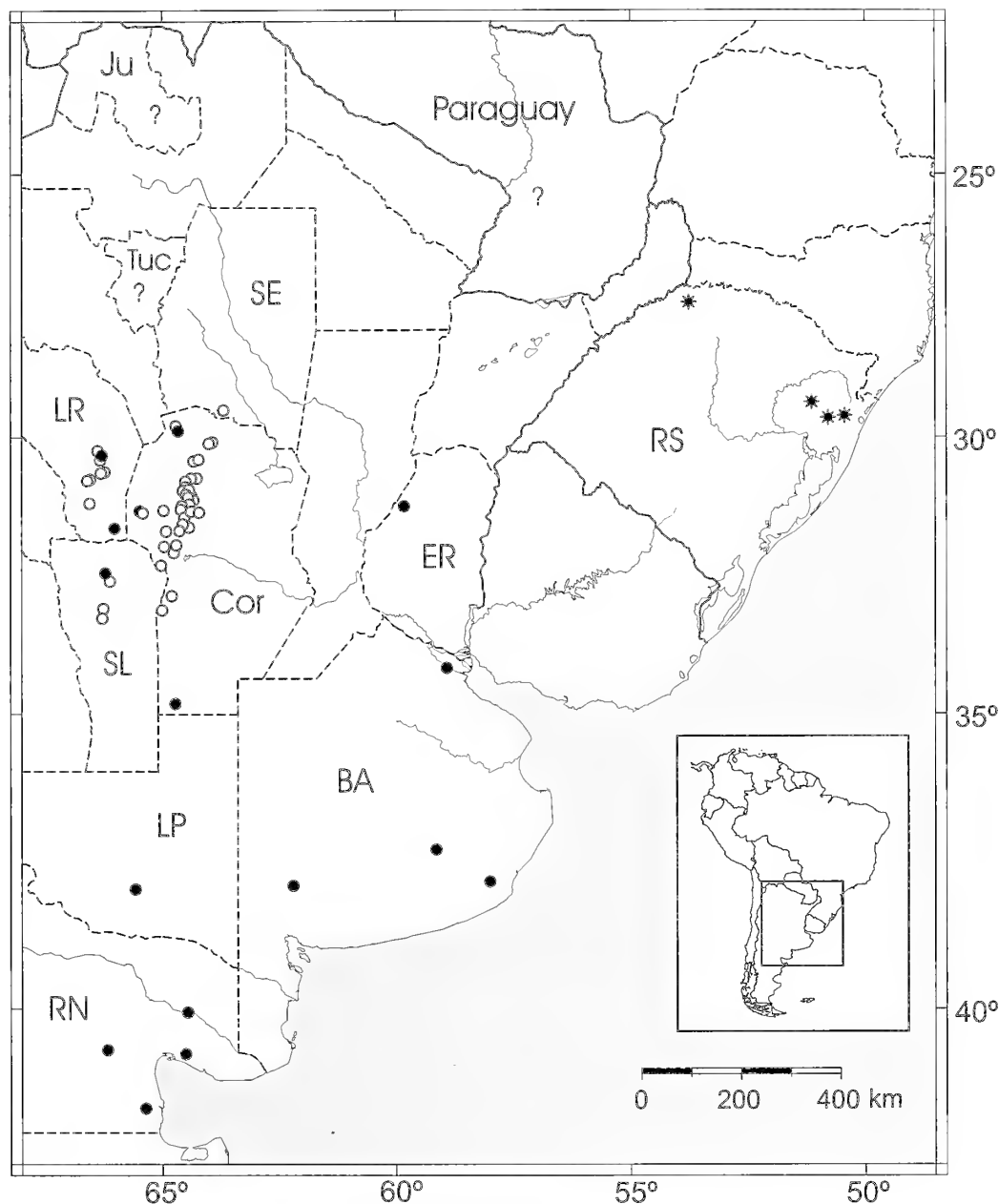


Figure 15.—Studied localities of *Zabius gauchus* new species (black stars), *Z. fuscus* (light circles), and *Z. birabeni* (black circles). Solid thick lines: country boundaries; thin lines: rivers; dashed lines: province or state boundaries. Abbreviations: Ju: province of Jujuy, Tuc: province of Tucumán, SE: province of Santiago del Estero, LR: province of La Rioja, ER: province of Entre Ríos, Cor: province of Córdoba, SL: province of San Luis, LP: province of La Pampa, BA: province of Buenos Aires, RN: province of Río Negro, RS: state of Rio Grande do Sul. Inset: location of the represented area.

examine several specimens from their collections. The senior author also thanks Camilo Mattoni and Alfredo Peretti for providing information on the capture site of *Zabius fuscus* in the Salinas Grandes area, and Michael Soleglad for fruitful discussion on the nomenclature of chelal carinae. The latter, Victor Fet, and two referees (Lorenzo Prendini, Erich Volschenk) made many useful suggestions to improve the manuscript. The collaborative work was facilitated through a travel grant to LEA (*Programa de Centros Asociados de Pós-graduação Brasil / Argentina, CAPES / SPU - Universidade Estadual de Campinas / Universidad Nacional de Córdoba*). Additional support was provided by Projeto Biota/Fapesp (# 99/05446-8 to ADB and DMC) and CNPq to ADB (grant #

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Revision of the spider genus *Taira* (Araneae, Amaurobiidae, Amaurobiinae)

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Abstract. The cribellate amaurobiid genus *Taira*, which is suggested to be most similar to the genus *Amaurobius* and some other related genera, is revised based on genital characters. Eight species, one from Japan and seven from China, are included. Five new species from China are described: *T. cangshan*, *T. concava*, *T. latilabiata*, *T. obtusa*, and *T. sulciformis*. *Titanoeca decorata* Yin & Bao 2001 is newly transferred to this genus and its male is described for the first time. *Taira lunaris* Wang & Ran 2004 is newly synonymized with *T. liboensis* Zhu, Chen & Zhang 2004.

Keywords: Genital structures, new species, China, Japan, synonymy

The amaurobiid genus *Taira* Lehtinen 1967, with the type species *T. flavidorsalis* (Yaginuma 1964), is restricted to Japan and South China. Only three species have been previously included in the genus, the type species, *T. liboensis* Zhu, Chen & Zhang 2004 and *T. lunaris* Wang & Ran 2004, both from Libo County, Guizhou Province of China (Zhu et al. 2004; Wang & Ran 2004).

Because the phylogeny of the family Amaurobiidae is poorly understood, the relationships of *Taira* with other amaurobiid genera are ambiguous. The inclusion of *Taira* and *Tamgrinia* Lehtinen 1967 in the same tribe Tairini of the subfamily Amaurobiinae by Lehtinen (1967) was questioned by Wang (2000). After comparing the ultrastructures of *Taira* and *Tamgrinia* with other amaurobiid genera [*Arctobius* Lehtinen 1967 (Arctobiinae), *Amaurobius* C.L. Koch 1837 (Amaurobiinae), *Callobius* Chamberlin 1947 (Amaurobiinae), *Pimus* Chamberlin 1947 (Amaurobiinae), *Coelotes* Blackwall 1841 (Coelotinae), and *Rubrius* Simon 1887 (Macrobininae)], Wang (2000) found that *Taira* is closer to *Ambaurobius* and allied genera (*Callobius* and *Pimus*) than *Tamgrinia*. The ultrastructural characters shared by *Taira* and *Amaurobius* and related genera that differ from those of *Tamgrinia* include: the striped small hood of the trichobothria, the presence of “amaurobiid ALS spigots” (named as “modified spigots” by Griswold et al. 2005) and the presence of paracribellar spigots on both the posterior lateral and posterior median spinnerets, while *Tamgrinia* have smooth small trichobothrial hoods and none of the spigots mentioned above (Wang & Ran 2004).

In this paper, the genus *Taira* is revised with particular attention to the genital structures. Eight species are recognized including five new species from China. The species *Titanoeca decorata* Yin & Bao 2001 is newly placed in this genus and its male is described for the first time. *Taira lunaris* is synonymized with *T. liboensis*.

METHODS

All specimens are preserved in 75% ethanol and were examined, illustrated, and measured using a Tech XTL-II stereomicroscope equipped with an Abbe drawing device. Eye sizes are measured as the maximum diameter from either above or in front. Leg measurements are shown as: total

length (femur, patella and tibia, metatarsus, tarsus). All measurements are in millimeters.

The distribution map was generated using GIS ArcView software and the .dbf files of the studied species are downloadable from <http://www.amaurobiidae.com>, which is published and maintained by Xin-Ping Wang.

The following abbreviations are used: Museum of Hebei University, Baoding, China (MHBU); the Collection of the Arachnological Society of Japan (CASJ) at Otemon Gakuin University, Osaka; Hunan Normal University, Changsha, China (HNUC).

Abbreviations used in this study are: ALE = anterior lateral eye; AME = anterior median eye; MOA = median ocular area; PLE = posterior lateral eye; PME = posterior median eye; DTA = dorsal tibial apophysis; RTA = retrolateral tibial apophysis.

TAXONOMY

Family Amaurobiidae Thorell 1870

Subfamily Amaurobiinae Thorell 1870

Taira Lehtinen 1967

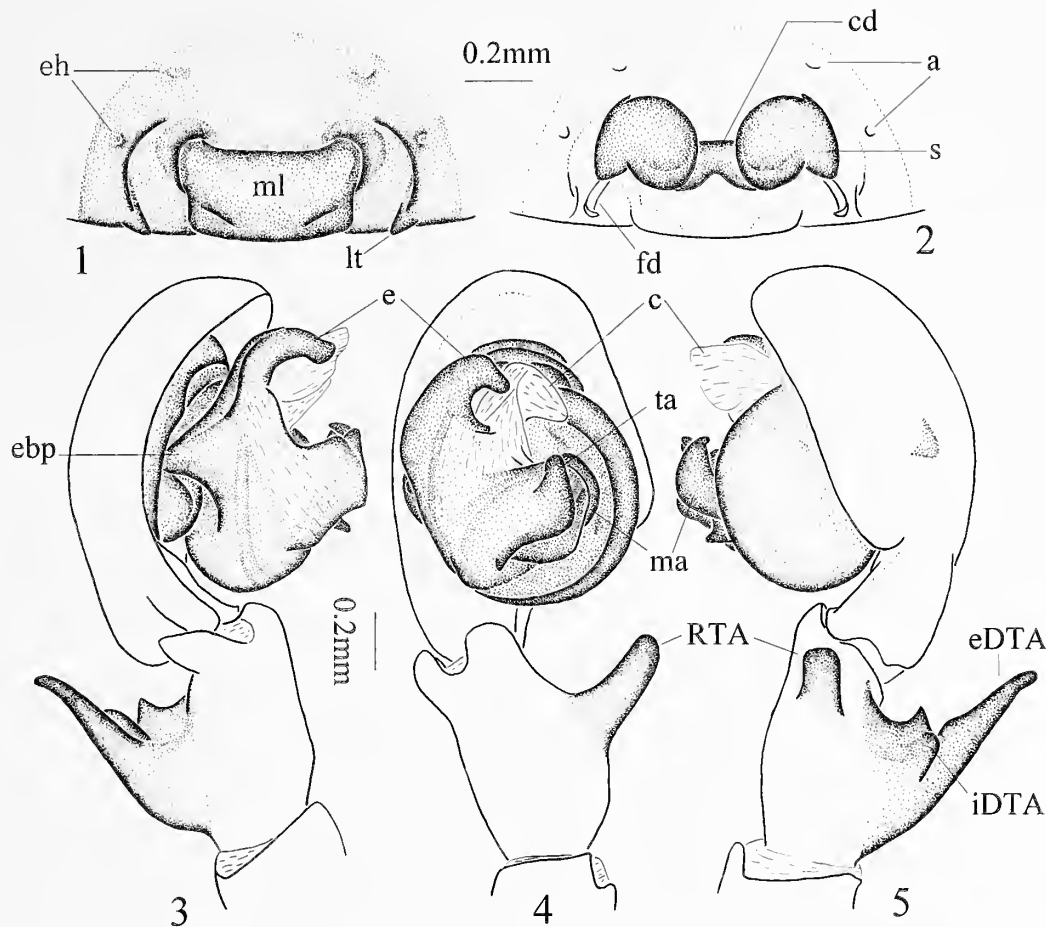
Taira Lehtinen 1967:266, 340.

Type species.—*Amaurobius flavidorsalis* Yaginuma 1964, by original designation.

Diagnosis.—This genus is similar to *Amaurobius*, but can be distinguished from the latter by the small RTA, the big interior branch and the relatively small exterior branch of the DTA (versus the small interior and big exterior branches of the DTA), the absence of an embolic basal process (except *T. liboensis*) (versus a dorsally pointed process, also indicated by Thaler & Knaflach (2000:341, figs. 19–22)), the big double membranous conductor (versus a single membrane), the scimitar-shaped median apophysis with the inflated base, the big, anteriorly pointed tegular process of the male palp, the wide epigynal teeth, and the retrolaterally curved fertilization ducts of the female epigynum (Figs. 1–5).

Description.—Carapace pear-shaped, with many black hairs. Cephalic area more or less elevated. Fovea longitudinal. Cervical groove and radial furrow distinct. Anterior eye row slightly retrocurved and posterior one procurved. MOA trapeziform, longer than wide or as long as wide. Chilum undivided. Chelicerae with distinct lateral condyles, 3 or 4

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Figures 1–5.—*Amaurobius fenestralis* (Ström 1768). Males and females from Denmark and Sweden (loaned from Zoological Museum, University of Copenhagen, Denmark and Naturhistoriska Riksmuseum, Stockholm, Sweden) 1. Female, epigynum. 2. Same, vulva. 3. Left palp of the male, prolateral view. 4. Same, ventral view. 5. Same, retrolateral view. Abbreviations: a = atrium; c = conductor; cd = copulatory duct; e = embolus; ebp = embolic basal process; eDTA = exterior branch of dorsal tibial apophysis; eh = epigynal hood; fd = fertilization duct; iDTA = interior branch of dorsal tibial apophysis; lt = lateral teeth; ma = median apophysis; ml = median lobe; ta = tegular apophysis; s = spermatheca; RTA = retrolateral tibial apophysis.

promarginal and 3 or 4 retromarginal teeth. The second promarginal tooth largest. Legs slightly slender (especially those of males), with 3 claws on the tarsi, many spines on femora, tibiae, and metatarsi. Metatarsus IV with a single row of setae making up the calamistrum (about half the length of the metatarsus IV), calamistrum of male more or less reduced. Leg formula: 1423 or 1243. Female palp with two claws on the end of tarsi, one of the paired claws lost. Abdomen oval, with some irregular black markings. Cribellum of female obviously divided and narrower than the width of anterior lateral spinnerets. Male cribellum somewhat reduced. Male palpal tibia with a strong RTA and a branched DTA. The interior branch of DTA well developed, sometimes with a groove on the prolateral view of left palp. And the exterior branch of it small, often depressed prolaterally. The cymbium modified retrolaterally, with a slightly narrow base and a blunt process pointing retrolaterally. Embolus wide, short, and flat, with slightly thin apex. Conductor membranous, doubled. Median apophysis scimitar-shaped, with an inflated base, originating on a membranous area of tegulum posteriorly. Tegulum with one or two big, anteriorly pointed processes. Female epigynum with two small hoods, a wide median lobe, and a pair of

epigynal teeth (the projections of epigynal cuticle) originating on the outside of median lobe. A pair of pores can be definitely located on the dorsal view of epigynum. Copulatory ducts lying between spermathecae and connected with each other. Spermathecae ball-like. Fertilization ducts originating behind the spermathecae and curved outwards.

Biology.—Species of this genus can be found under stones, tree bark, and caves or in rock crevices. The web is small, with one or more retreat(s) on the web mesally.

Distribution.—Members of the genus *Taira* are restricted to East Asia, including South China and Japan (Fig. 41).

Relationships with other amaurobiine genera.—In order to evaluate the relationships of *Taira* and other amaurobiine genera, some specimens of *Amaurobius*, *Callobius*, and *Tamgrinia* were examined, as well as some literature sources (e.g., Lehtinen 1967; Leech 1972; Wang 2000).

We support the conclusion of Wang (2000) that the genus *Taira* is phylogenetically far from *Tamgrinia* and more similar to *Amaurobius*, *Callobius*, and *Pinnus*. Wang & Ran (2004) indicated that the genus *Taira* can be distinguished from *Tamgrinia* at least by the following characters: the undivided chilum, the transversely striped cephalothorax, the large

trichobothrial hoods, the presence of "modified spigots," and the paracribellar spigots. As far as genital characters are concerned, the differences between *Taira*, *Amaurobius*, *Callobius*, and *Pimus* with *Tangrinia* include: the absence of an embolic supporter and tegular membranous apophysis, the unsclerotized conductor of the male palp, the epigynal atrial split, the absence of a septal sclerite, the connected copulatory ducts, and the nearly ball-like spermathecae of the female epigynum.

The features shared by *Taira*, *Amaurobius*, *Callobius*, and *Pimus* are: the striped small hood of the trichobothria, the presence of "modified spigots," and the presence of paracribellar spigots on both posterior lateral spinnerets and

posterior median spinnerets (Wang & Ran 2004). Another structure shared by these genera is the undivided chilum.

After comparing the genital structures of *Taira* with *Amaurobius*, *Callobius*, and *Pimus*, we regard *Taira* as most similar to *Amaurobius* because of the following shared characters: the presence of RTA and the branched DTA, the short embolus, the membranous conductor, the posteriorly originated median apophysis, the presence of a tegular process on the male palp, the wide median lobe, the presence of epigynal teeth, the nearly spherical shaped spermathecae and the positions of the copulatory ducts of the female epigynum.

KEY TO SPECIES OF THE GENUS *TAIRA*

1. Female 2
Male (those of *T. obtrusa* and *T. latilabiata* unknown) 9
2. Median septum with width less than 2 times length (Figs. 7, 36) 3
Median septum with width at least 2 times length (Figs. 12, 17, 22, 27, 29, 34) 4
3. Median septum with the widest mid-part (Fig. 36) *T. sulciforis*
Median septum with the widest anterior edge (Fig. 7) *T. flavidorsalis*
4. Median septum with width about 4 times length (Fig. 12) *T. cangshan*
Median septum with width less than 3 times length (Figs. 17, 22, 27, 29, 34) 5
5. Median septum small, slightly pointed posteriorly (Fig. 17) *T. concava*
Median septum large, not pointed posteriorly (Figs. 22, 27, 29, 34) 6
6. Spermathecae small, widely separated (Fig. 28) *T. latilabiata*
Spermathecae big, narrowly separated (Figs. 23, 30, 35) 7
7. Epigynal teeth with wide posterior margin (Fig. 34) *T. obtrusa*
Epigynal teeth with a tip end (Figs. 22, 29) 8
8. Spermathecae with sharp anterior margin (Fig. 23) *T. decorata*
Spermathecae with blunt anterior margin (Fig. 30) *T. liboensis*
9. DTA far away from tibia (Figs. 11, 21, 26, 33, 40) 10
DTA close to tibia (Fig. 16) *T. cangshan*
10. DTA with sharp exterior branch and normal interior one (Fig. 31) *T. liboensis*
DTA not with sharp exterior branch, with grooved interior one (Figs. 9, 19, 24, 38) 11
11. DTA with interior branch as long as wide (Fig. 38) *T. sulciforis*
DTA with interior branch much longer than wide (Figs. 9, 19, 24) 12
12. RTA big (Figs. 20, 21) *T. concava*
RTA small (Figs. 10, 25) 13
13. Embolic end wide (Fig. 25) *T. decorata*
Embolic end narrow (Fig. 10) *T. flavidorsalis*

Taira flavidorsalis (Yaginuma 1964)

Figs. 6–11, 41

Amaurobius flavidorsalis Yaginuma 1964:20, figs. 1–5; Yaginuma 1971:128, figs. 107.1–3; Yaginuma 1986:9, fig. 7.3; Chikuni 1989:21, fig. 1.

Taira flavidorsalis (Yaginuma): Lehtinen 1967:266, figs. 204, 207.

Material examined.—*Holotype*: JAPAN: *Hiroshima Prefecture*: male, Mt. Azuma (35°00'N, 133°00'E), 15 August 1963, Y. Morinaga (CASJ).

Paratype: JAPAN: *Tottori Prefecture*: 1 female, Mt. Daisen (35°12'N, 133°21'E), July 1937, M. Tanaka (CASJ).

Diagnosis.—This species is similar to *T. concava* (Figs. 17–21), but can be distinguished from the latter by the small and ventrally originated RTA, the narrow furrow of interior branch of DTA, the less depressed exterior branch of DTA, the thin apex of embolus, the small conductor, the slightly inflated base of median apophysis, and the sunken apex of tegular process of male palp. Also, the same relative shape of

the median lobe, the mesally situated copulatory ducts, and the nearly elliptical spermathecae of the female epigynum.

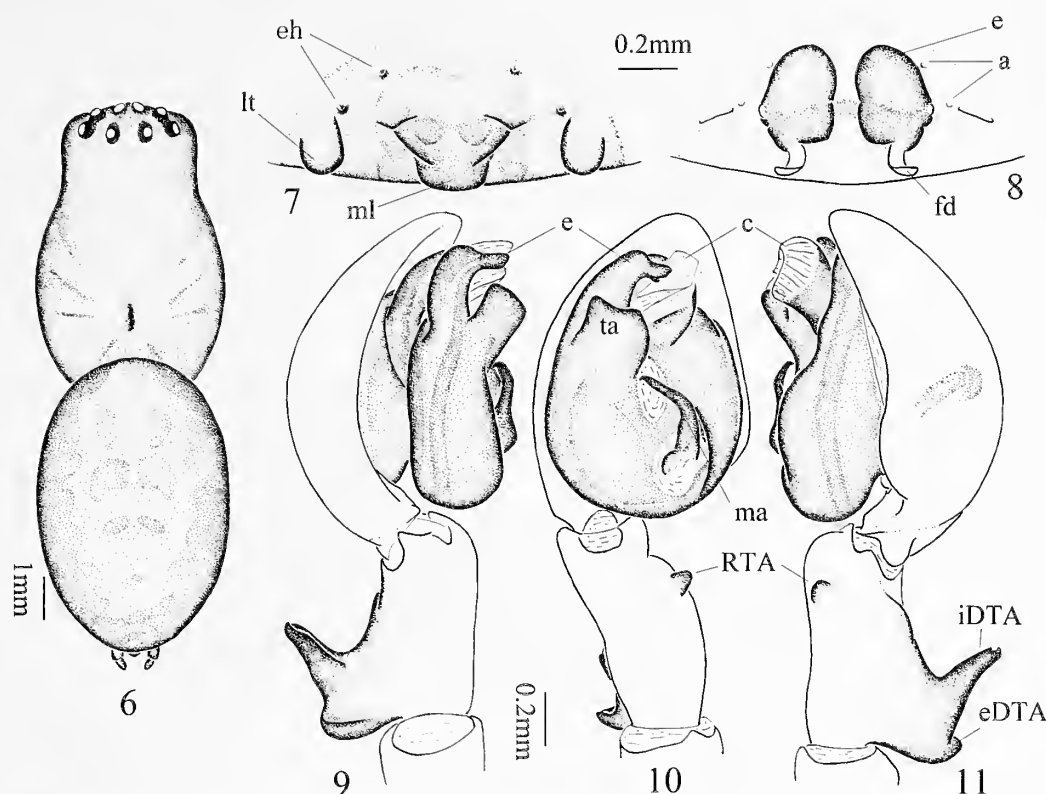
Redescription.—Cheliceral promargin with three teeth, retromargin with four.

Male palp (Figs. 9–11) with a small and ventrally originated RTA and a big DTA. The interior branch of DTA long, anterodorsally pointed, with a narrow furrow. The exterior branch of DTA small, depressed prolaterally and pointed dorsally. The base of cymbium narrow and modified retrolaterally. Embolus originated prolaterally, short, flat and slightly curved, with a thin apex. Conductor membranous and doubled. Median apophysis situated posteriorly, with an acute tip and inflated base. Tegular process close to the base of embolus, with a sunken apex.

Female epigynum (Figs. 7–8) with a big median lobe. Epigynal teeth originated retrolaterally, with blunt apex. Copulatory ducts small, between the spermathecae. Spermathecae nearly elliptical.

For further detail, see Yaginuma (1964).

Distribution.—This species has been found in Japan (*Hiroshima*, *Tottori*) (Fig. 41).



Figures 6–11.—*Taira flavidorsalis* (Yaginuma 1964). 6. Male body, dorsal view. 7. Female, epigynum. 8. Same, vulva. 9. Left palp of the male, prolateral view. 10. Same, ventral view. 11. Same, retrolateral view.

Remarks.—Judging from the publication (Wang & Ran 2004: 31, figs. 5–6), the specimen illustrated as *T. flavidorsalis* is misidentified. Further examination of this specimen is badly needed in order to determine its species status.

***Taira cangshan* new species**
Figs. 12–16, 41

Material examined.—*Holotype*: CHINA: Yunnan: male, Dali, Mt. Cangshan (25°58'N, 99°52'E), Yudailu, elev. 2400 m, 1 January 2004, Zi-Zhong Yang (MHBUS).

Paratypes: CHINA: Yunnan: two females, the same location as holotype, 24 October 2004, Hai-bo Pu and Zi-Zhong Yang (MHBUS).

Other material examined: 7 ♀, Lushui, Pianma (26°01'N, 98°37'E), elev. 2200 m, Yunnan, 9 May 2004, Zhi-Sheng Zhang and Zi-Zhong Yang (MHBUS).

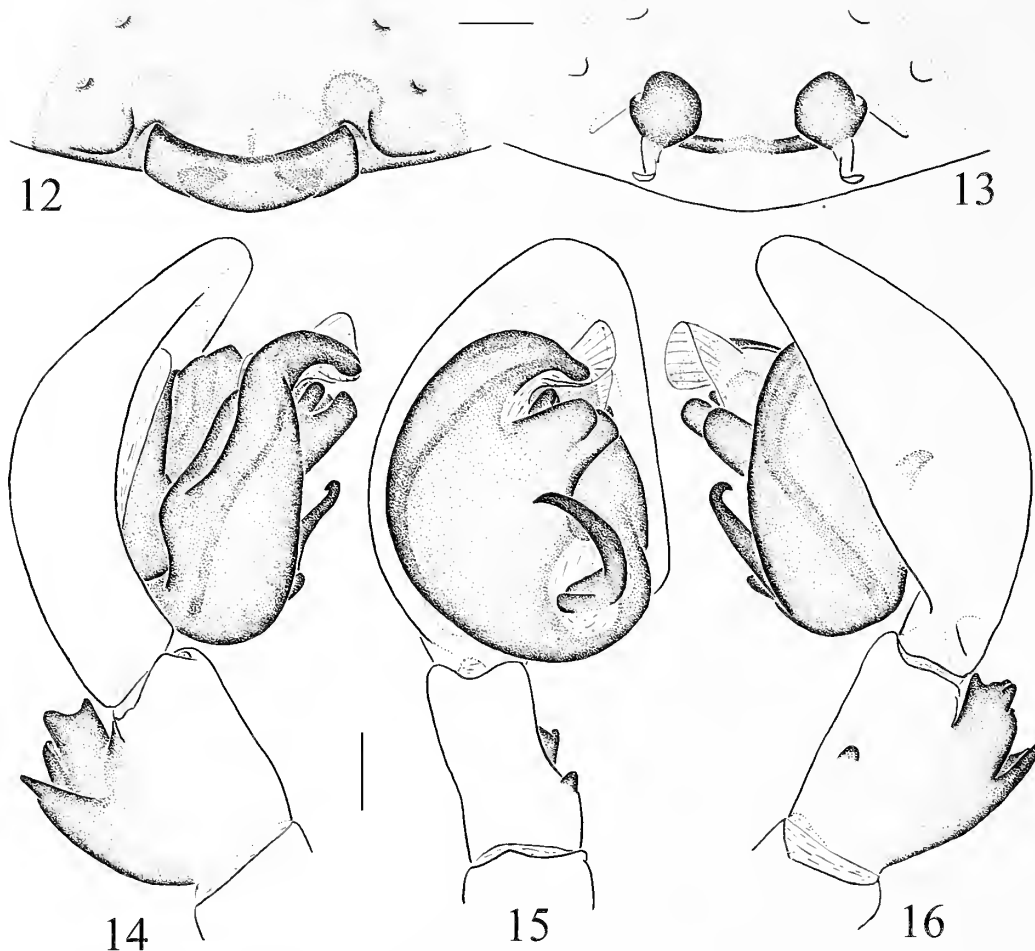
Etymology.—The specific name refers to the type locality and is a noun in apposition.

Diagnosis.—The male palpal tibial apophyses of the new species are different from other *Taira* species: RTA small, DTA located distally. But the palpal organ and epigynum are similar to the others. It can be distinguished from the type species, *T. flavidorsalis* (Figs. 7–11) by the blunt apex of embolus, the acute tip of median apophysis, the bifurcated tegular apophysis of male palpal bulb; the epigynal median lobe that is four times wider than long and procurved, the wide base of the epigynal teeth, the slender copulatory ducts and the small spermathecae.

Description.—*Male (holotype)*: Total length 6.43: prosoma 3.16 long, 2.24 wide; opisthosoma 3.57 long, 2.50 wide. Prosoma yellow, with yellow brown anterior and retrolateral

areas. Eye sizes and interdistances: AME 0.15, ALE 0.15, PME 0.13, PLE 0.15; AME–AME 0.05, AME–ALE 0.10, PME–PME 0.20, PME–PLE 0.25, ALE–PLE 0.08. MOA 0.50 long, front width 0.33, base width 0.45. Clypeus height 0.25. Chelicerae brown, with 4 promarginal and 3 retromarginal teeth. Labium brown. Endites yellow brown. Sternum deep yellow. Leg measurements: I 14.28 (4.59, 4.79, 3.37, 1.53), II 9.49 (2.86, 3.37, 2.14, 1.12), III 7.86 (2.45, 2.65, 1.84, 0.92), IV 9.58 (2.75, 3.26, 2.45, 1.12). Leg formula: 1423. Opisthosoma gray yellow, with indistinct 3 chevron-like markings dorsally. Palp (Figs. 14–16) with a small RTA, located near the base of tibia. DTA relatively small, close to the anterior part of tibia dorsally. Interior branch short and strong, with a bifurcated apex. Exterior branch small, with an acute tip, pointing anterodorsally. The anterior part of embolus relatively thin. Conductor membranous and doubled. Median apophysis with a bulbous base and arcuate anterior part. Tegulum bifurcated, pointing antero-retrolaterally.

Female: Total length 6.83–8.77. A female (one of the paratypes) total length 8.06: prosoma 3.57 long, 2.55 wide; opisthosoma 4.79 long, 3.26 wide. Eye sizes and interdistances: AME 0.15, ALE 0.18, PME 0.13, PLE 0.15; AME–AME 0.08, AME–ALE 0.20, PME–PME 0.28, PME–PLE 0.38, ALE–PLE 0.10. MOA 0.55 long, front width 0.38, back width 0.53. Clypeus height 0.33. Leg measurements: I 10.51 (2.96, 3.67, 2.45, 1.43), II 8.47 (2.45, 3.06, 1.84, 1.12), III 7.24 (2.24, 2.45, 1.63, 0.92), IV 9.07 (2.65, 3.16, 2.24, 1.02). Leg formula and other characters as the male holotype. Epigynum (Figs. 12, 13) with a wide median lobe, 4 times wider than long and curved posteriorly. Epigynal teeth with wide base. Copulatory ducts slender, between spermathecae. Spermathecae ball-like, widely separated.



Figures 12–16.—*Taira cangshan* new species. 12. Female, epigynum. 13. Same, vulva. 14. Left palp of the male, prolateral view. 15. Same, ventral view. 16. Same, retrolateral view. Scale lines: 0.2 mm.

Distribution.—*Taira cangshan* is found in China (Yunnan) (Fig. 41).

Habitat.—Specimens have been found under stones, with a small irregular web.

Taira concava new species

Figs. 17–21, 41

Material examined.—*Holotype*: CHINA: *Sichuan*: male, Mt. Emei (29°32'N, 103°19'E), elev. ~ 1600 m, 16 September 2004, matured at the end of October 2004, Zhi-Sheng Zhang (MHBU).

Paratype: CHINA: *Sichuan*: 1 female, collected with holotype (MHBU).

Etymology.—The specific name is Latin, meaning depressed and refers to the depressed exterior branch of DTA.

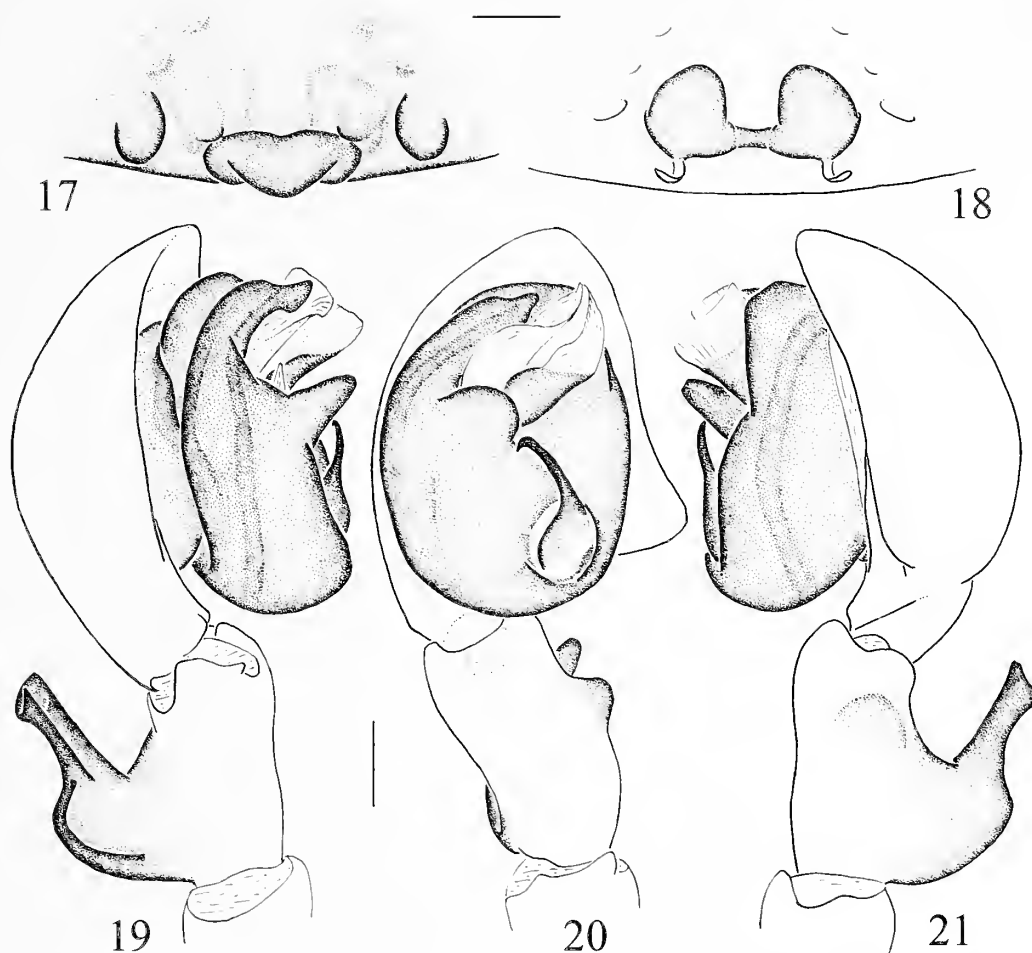
Diagnosis.—The new species is similar to *T. sulcifformis* (Figs. 36–40), but can be distinguished from the latter by the narrow interior branch of DTA, obviously depressed exterior branch of DTA, the relatively thin and long median apophysis, the blunt tegular apophysis of male palp; the wider than long median lobe and the short copulatory ducts of female epigynum.

Description.—*Male holotype*: Total length: 4.74, prosoma 2.19 long, 1.58 wide; opisthosoma 2.70 long, 1.79 wide. Prosoma yellow, with many tiny black markings. Eye sizes and

interdistances: AME 0.08, ALE 0.13, PME 0.10, PLE 0.10. AME–AME 0.10, AME–ALE 0.10, PME–PME 0.13, PME–PLE 0.20, ALE–PLE 0.05. MOA 0.33 long, front width 0.25, back width 0.33. Clypeus height 0.20.

Chelicerae yellow brown, with 4 promarginal and 3 retro-marginal teeth. Endites deep yellow, labium dark yellow. Sternum dark yellow. Leg measurements: I 10.51 (2.75, 3.67, 2.81, 1.28), II 7.85 (2.24, 2.65, 1.99, 0.97), III 6.23 (1.84, 2.04, 1.58, 0.77), IV 7.55 (2.19, 2.45, 1.99, 0.92). Leg formula: 1243. Opisthosoma grey brown, with a pair of sigilla and indistinct 3 chevron-like markings. Palpal tibia with a big, ball-like RTA and wide DTA. The interior branch of DTA long and thin, with a furrow and the exterior branch of it wide, with an obvious pit. The base of cymbium narrow and modified. Embolus with thin apex. Conductor big, membranous and doubled. Median apophysis slender, with an inflated base. Tegulum with a blunt process (Figs. 19–21).

Female paratype: Total length 5.30: prosoma 2.30 long, 1.58 wide; opisthosoma 3.16 long, 2.30 wide. Eye area too badly damaged to be measured. Leg measurements: I 6.07 (1.73, 2.14, 1.38, 0.82), II 4.84 (1.43, 1.68, 1.07, 0.66), III 4.18 (1.27, 1.43, 0.92, 0.56), IV 5.25 (1.58, 1.84, 1.17, 0.66). Leg formula: 1423. Epigynum with a small median lobe that is far wider than long. Epigynal teeth widely separated, with blunt apex.



Figures 17–21.—*Taira concava* new species. 17. Female, epigynum. 18. Same, vulva. 19. Left palp of the male, prolateral view. 20. Same, ventral view. 21. Same, retrolateral view. Scale lines: 0.2 mm.

Copulatory ducts thin and short. Spermathecae ball-like (Figs. 17, 18).

Distribution.—This species is found in China (Sichuan) (Fig. 41).

Habitat.—Specimens have been found within crevices of cliffs or under rocks.

***Taira decorata* (Yin & Bao 2001) new combination**

Figs. 22–26, 41

Titanoeca decorata Yin & Bao 2001:60, figs. 2a–e.

Type specimens.—*Holotype*: CHINA: *Hunan*: female, Mt. Mangshan, Yizhang County, (24°59'N, 112°50'E), 18 May 1999, Jian-Hui Yang (HNUC) (not examined).

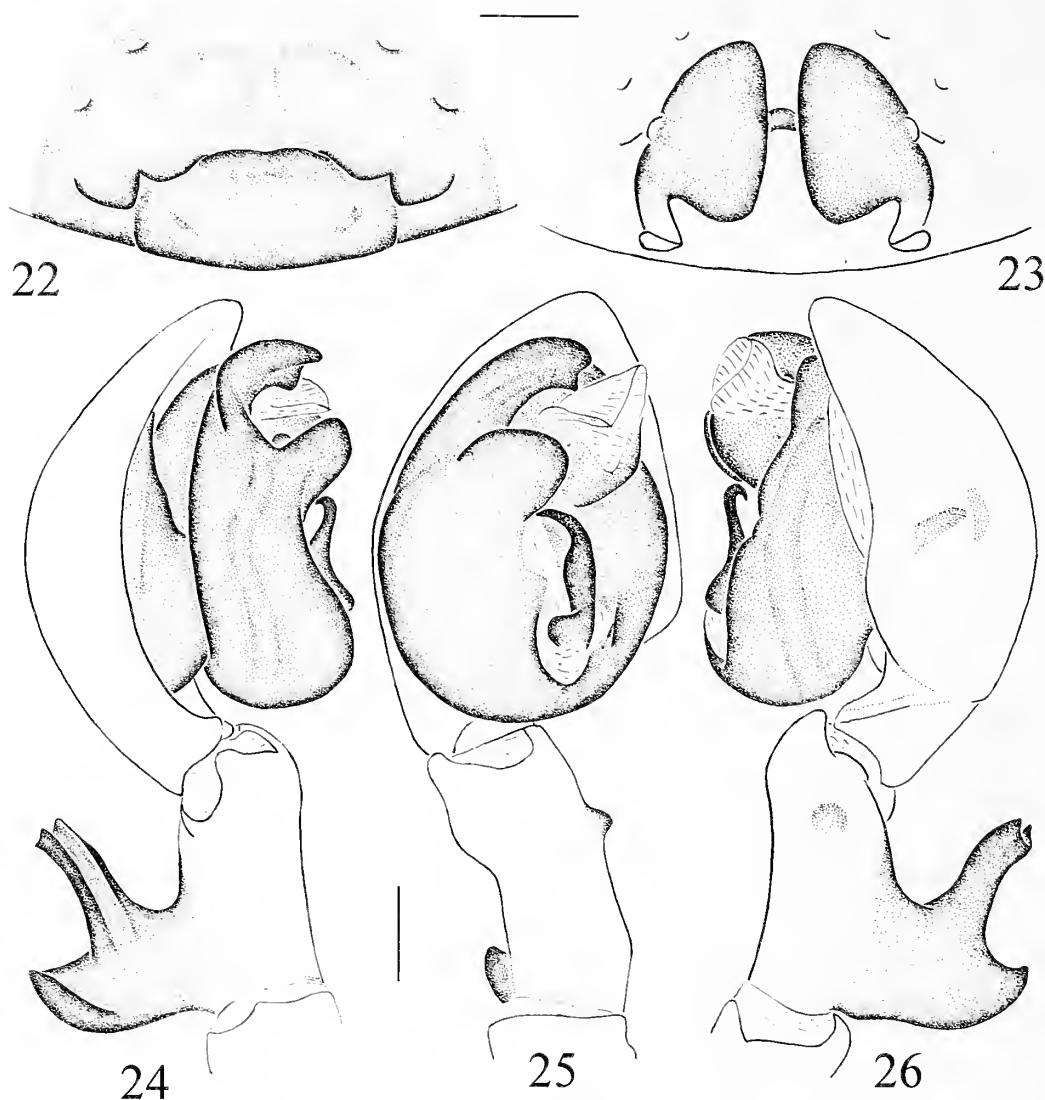
Material examined.—CHINA: *Fujian*: 1 ♂, 3 ♀, Moshikeng, Mt. Wuyi (26°54'N, 116°42'E), 20 May 2004, Feng Zhang (MHB); 1 ♂, 8 ♀, between Guadun and Tongmu, Mt. Wuyi, 24 May 2004, Feng Zhang (MHB); 6 ♀, Guadun, Mt. Wuyi, 23 May 2004, Feng Zhang (MHB); 3 ♀, Mt. Wuyi, 10 July 1986, Ming-Sheng Zhu (MHB).

Diagnosis.—This species is similar to *T. flavidorsalis* (Figs. 7–11), but can be distinguished from the latter by the narrow sulciform interior branch of DTA, the slightly bifurcated embolus, the prolaterally outstanding median part of median apophysis, the blunt tegulum of male palp; the wide median lobe of epigynum, the small epigynal teeth, the

epigynal hood far away from the epigynal teeth and the slightly peaked spermathecae anteriorly.

Description.—*Male*: Total length: 4.18–4.44. One male total length 4.44: prosoma 2.40 long, 1.79 wide; opisthosoma 2.14 long, 1.53 wide. Prosoma yellow, with dark yellow Cephalic area. Eye sizes and interdistances: AME 0.10, ALE 0.15, PME 0.13, PLE 0.15; AME–AME 0.08, AME–ALE 0.10, PME–PME 0.15, PME–PLE 0.20, ALE–PLE 0.08. MOA 0.43 long, front width 0.28, back width 0.40. Clypeus height 0.13. Chelicerae yellow brown, with 4 promarginal and 3 retromarginal teeth. Labium and endites deep yellow. Sternum yellow, with deep yellow lateral margin. Leg measurements: I 11.63 (3.11, 4.08, 3.11, 1.33), II 7.75 (2.24, 2.70, 1.99, 0.82), III 6.22 (1.89, 2.04, 1.58, 0.71), IV 7.70 (2.19, 2.60, 2.09, 0.82). Leg formula: 1243. Opisthosoma yellowish, with many white hairs and many irregular markings, a pair of yellow longitudinal markings and indistinct 4 chevron-like markings. Cardiac markings red. Palpal tibia with a small RTA, located on the anterior part of tibia. The interior branch of DTA with a narrow groove and the exterior branch depressed in prolateral view. Embolus bifurcated anteriorly. Conductor membranous and doubled. Median apophysis inflated in the middle part. Tegular process blunt (Figs. 24–26).

Female: Epigynum with wide median lobe. Epigynal teeth close to the lateral margins of median lobe. Copulatory ducts thin and short. Spermathecae peaked anteriorly. Fertilization



Figures 22–26.—*Taira decorata* (Yin & Bao 2001). 22. Female, epigynum. 23. Same, vulva. 24. Left palp of the male, prolateral view. 25. Same, ventral view. 26. Same, retrolateral view. Scale lines: 0.2 mm.

ducts originating on the spermathecae posteriorly and curved retrolaterally (Figs. 22, 23).

For further details, see Yin & Bao (2001).

Distribution.—*Taira decorata* has been found in China (Zhejiang, Fujian and Hunan) (Fig. 41).

Remarks.—This species was first described by Yin & Bao (2001) based on female specimens collected from Mt. Mangshan of Hunan Province and Mt. Fengyuan (28°06'N, 119°06'E) of Zhejiang Province and placed in the genus *Titanoeca* of the family Titanoecidae. After comparing the original figures with the specimens we collected from Mt. Wuyi of Fujian, we have determined that they are the same species though the type specimens are unavailable. Moreover, Mt. Wuyi is situated between Mt. Mangshan and Mt. Fengyuan.

***Taira latilabiata* new species**

Figs. 27, 28, 41

Material examined.—*Holotype*: CHINA: *Guizhou*: female, Weining, Chaohai National Natural Reserve (26°51'N, 104°15'E), 2 July 2005, Hui-Ming Chen (MHBU).

Paratypes: CHINA: *Guizhou*: 6 females, collected with holotype (MHBU).

Etymology.—The specific name, derived from Latin adjective “*latilabiatus*,” refers to the wide and labiate median lobe of the female epigynum.

Diagnosis.—The new species is similar to *T. liboensis* (Figs. 29, 30), but differs from the latter by the wide epigynal median lobe, the long copulatory ducts and the relatively small spermathecae.

Description.—*Female*: total length 7.04–7.75. Holotype total length 7.75: prosoma 3.47 long, 2.35 wide; opisthosoma 4.39 long, 3.06 wide. Prosoma brown, with many black hairs and a “V” shaped yellow marking in front of the fovea and behind MOA. Eye sizes and interdistances: AME 0.15, ALE 0.18, PME 0.15, PLE 0.18; AME–AME 0.08, AME–ALE 0.13, PME–PME 0.20, PME–PLE 0.30, ALE–PLE 0.13. MOA 0.55 long, front width 0.35, back width 0.50. Clypeus height 0.20. Chelicerae brown, with 4 promarginal and 3 or 4 retromarginal teeth. Labium yellow brown. Sternum deep yellow. Legs yellow, with 2 blackish annular markings on



Figures 27, 28. *Taira latilabiata* new species. 27. Female, epigynum. 28. Same, vulva. Scale lines: 0.2 mm.

femora. Leg measurements: I 9.79 (2.75, 3.47, 2.14, 1.43), II 7.96 (2.35, 2.86, 1.63, 1.12), III 7.14 (2.24, 2.45, 1.53, 0.92), IV 9.07 (2.65, 3.16, 2.14, 1.12). Leg formula: 1423. Opisthosoma grey black, with yellowish markings and indistinct 3 chevron-like markings dorsally. Epigynum with a wide labiate median lobe and a pair of epigynal teeth. Two pairs of epigynal hoods situated in front of epigynal teeth. Copulatory ducts located between spermathecae and connected to each other. Spermathecae ball-like (Figs. 27, 28).

Male: unknown.

Distribution.—*Taira latilabiata* is known only from Guizhou province in China (Fig. 41).

Taira liboensis Zhu, Chen & Zhang 2004

Figs. 29–33, 41

Taira liboensis Zhu, Chen & Zhang 2004 (January):61, figs. 1A–F.

Taira lunaris Wang & Ran 2004 (March):31, figs. 1–4 (female holotype and paratype from Yueliang Cave, Libo, Guizhou, China, deposited in the Institute of Zoology, Beijing, China, not examined). **New synonymy.**

Material examined.—*Holotype*: CHINA: *Guizhou*: female, Shuijiang Cave, Libo (25°24'N, 107°52'E), 8 July 2001, Hui-Ming Chen (MHBU).

Paratypes: CHINA: *Guizhou*: 3 males, 2 females, same data as holotype (MHBU).

Other material: CHINA: *Guizhou*: 1 ♀, Shuijiang Cave, September 1998, Hui-Ming Chen (MHBU); 3 ♂, 1 ♀, Heshang Cave, Guiyang (26°35'N, 106°42'E), 13 May 1998, Hui-Ming Chen (MHBU); *Sichuan*: 1 ♂, 2 ♀, Mt. Emei (29°32'N, 103°19'E), elev. ~ 800 m, 16 September 2004, Zhi-Sheng Zhang (MHBU).

Diagnosis.—This species can be easily distinguished from the other *Taira* species by the indistinct RTA, the peaky interior branch of the DTA, the undepressed exterior branch of the DTA, the presence of the embolic process and two tegular processes of the male palp. It differs from *T. flavidorsalis* (Yaginuma 1964) (Figs. 7–11) by the wide apex of the male palpal embolus, the wide median lobe, and the long distances between the epigynal teeth and median lobe.

Redescription.—Cheliceral promargin with four teeth, retro-marginal with three.

Male: palp (Figs. 31–33) with indistinct RTA. Interior branch of DTA peaky, without groove, a small process located near the base of DTA in the prolateral view. Exterior branch of DTA small. Embolus with a basal process. Conductor membranous and doubled. Median apophysis thin, relatively long, arcuate curved, with an acute tip and an inflated base.

Tegulum with two processes near the apex of median apophysis.

Female: epigynum (Figs. 29, 30) with a brownish labiate median lobe. Epigynal teeth with wide base and slightly peaky tip. Two pairs of hoods situated in front of the epigynal teeth. Copulatory ducts short, connected to each other. Spermathecae nearly elliptical.

For further details, see Zhu et al. (2004).

Distribution.—*Taira liboensis* has been found in China (Guizhou, Sichuan) (Fig. 41).

Remarks.—*Taira liboensis* and *T. lunaris* were both published in 2004 in different journals. The former was published in January 2004 (indicated in the page header of the printed paper), while the latter, published in the *Bulletin of the British Arachnological Society* was published in March 2004 (personal communication with Ian Dawson, the Secretary of the British Arachnological Society). Therefore, the latter is a junior synonym.

Taira obtusa new species

Figs. 34, 35, 41

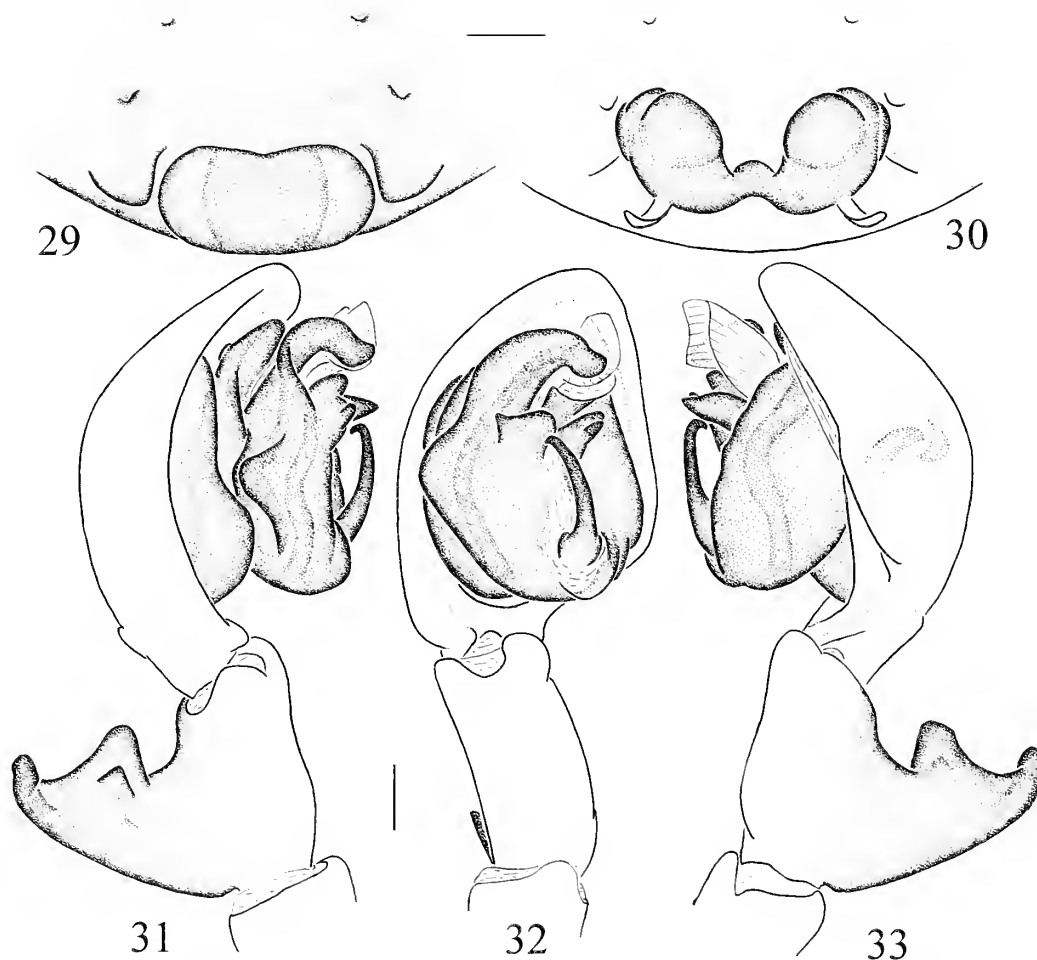
Material examined.—*Holotype*: CHINA: *Hubei*: female, Shennongjia National Nature Reserve (31°28'N, 110°22'E), Yazikou, 4 September 2004, Zhi-Sheng Zhang & Hui-Ming Chen (MHBU).

Paratypes: 11 females, collected with holotype (MHBU); *Guizhou*: 2 females, Mt. Fanjin (27°55'N, 108°41'E), Huixiangpin to Yu'ao, 2 August 2001, Jun-Xia Zhang & Zhi-Sheng Zhang (MHBU).

Etymology.—The specific name comes from the Latin word “*obtusus*,” meaning “blunt,” referring to the blunt end of the epigynal teeth.

Diagnosis.—The female of the new species is similar to that of *T. decorata* (Yin & Bao 2001) (Figs. 22, 23), but can be distinguished from the latter by the anteriorly and laterally extended median lobe of epigynum, the big blunt epigynal teeth, the wide copulatory ducts and the shape of the spermathecae.

Description.—*Female*: total length 6.50–7.50. Holotype total length 6.83: prosoma 3.06 long, 1.94 wide; opisthosoma 4.08 long, 2.96 wide. Prosoma yellow brown with dark brown lateral margins. Eye sizes and interdistances: AME 0.10, ALE 0.15, PME 0.13, PLE 0.15; AME–AME 0.08, AME–ALE 0.18, PME–PME 0.20, PME–PLE 0.25, ALE–PLE 0.08. MOA 0.48 long, front width 0.30, back width 0.43. Clypeus height 0.20. Chelicerae brown, with 4 promarginal and 3 retromarginal teeth. Endites dark yellow, labium brown. Sternum yellow, with yellowish margin. Leg measurements: I



Figures 29–33.—*Taira liboensis* Zhu, Chen & Zhang 2004. 29. Female, epigynum. 30. Same, vulva. 31. Left palp of the male, prolateral view. 32. Same, ventral view. 33. Same, retrolateral view. Scale lines: 0.2 mm.

8.47 (2.35, 2.96, 2.04, 1.12), II 6.73 (2.04, 2.24, 1.53, 0.92), III 5.51 (1.73, 1.84, 1.33, 0.61), IV 7.14 (2.04, 2.55, 1.73, 0.82). Leg formula: 1423. Opisthosoma yellowish, with many irregular black markings, a pair of cardiac markings and four indistinct chevron-like markings. Epigynum (Figs. 34–35) with antero-laterally extended trapeziform median lobe. Epigynal teeth with narrow base and wide body. Copulatory ducts located between spermathecae posteriorly. Spermathecae narrow anteriorly.

Male: unknown.

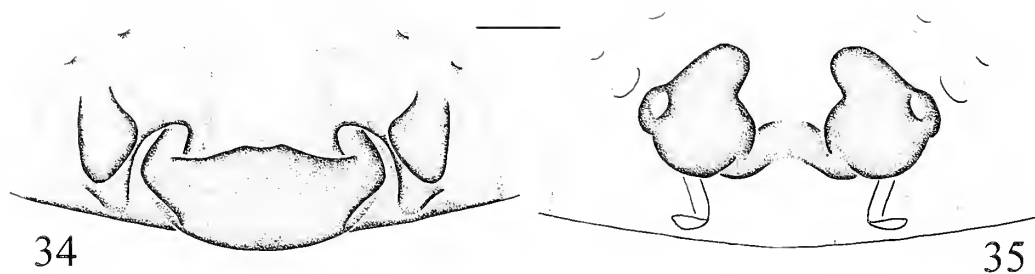
Distribution.—*Taira obtusa* is found in China (Hubei, Guizhou) (Fig. 41).

Habitat.—Specimens have been found within crevices of rocks.

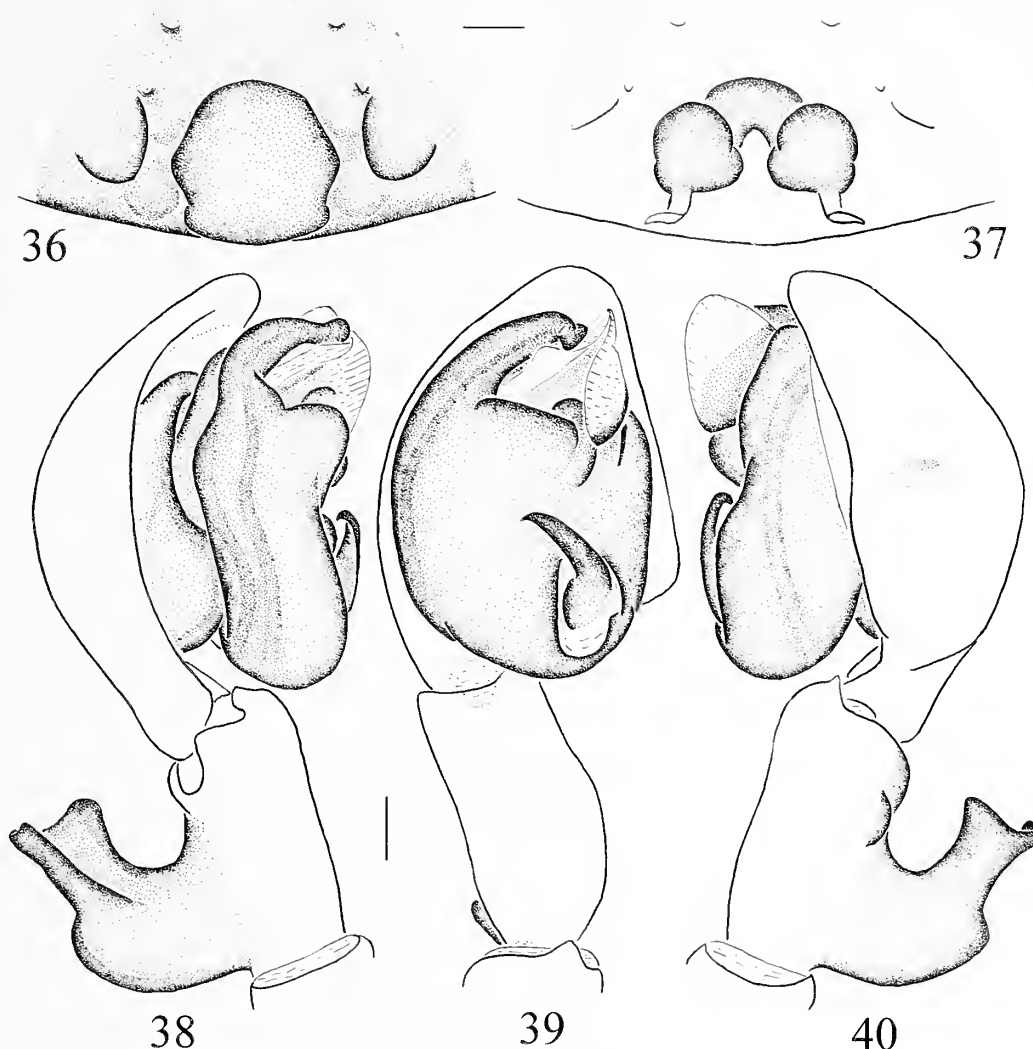
Taira sulciformis new species
Figs. 36–40, 41

Material examined.—*Holotype*: CHINA: *Fujian*: male, Mt. Wuyi (26°54'N, 116°42'E), Tongmu, 16 May 1985, Ming-Sheng Zhu (MHBUS).

Paratypes: CHINA: *Fujian*: 1 male, 4 females, collected with holotype (MHBUS); 1 female, Mt. Wuyi, Tongmu, 19 July 2003, Chao Zhang (MHBUS).



Figures 34, 35.—*Taira obtusa* new species. 34. Female, epigynum. 35. Same, vulva. Scale lines: 0.2 mm.



Figures 36–40.—*Taira sulciformis* new species. 36. Female, epigynum. 37. Same, vulva. 38. Left palp of the male, prolateral view. 39. Same, ventral view. 40. Same, retrolateral view. Scale lines: 0.2 mm.

Etymology.—The specific name is a combination of “*sulc-*” and “*-formis*.” The former means “groove,” and the latter means “with ... shape.” The combination refers to the obvious wide and big groove of the interior branch of DTA.

Diagnosis.—The new species is similar to *T. concava* (Figs. 17–21), but can be distinguished from the latter by the wide interior branch of DTA, indistinct depression of exterior branch of DTA prolaterally, the ventrally curved apex of embolus, the short median apophysis, the wide and flat tegular apophysis of the male palp; the longer median lobe, the wide and anteriorly curved copulatory ducts of female epigynum.

Description.—*Male*: total length 6.02–6.22. Holotype total length 6.22: prosoma 3.26 long, 2.24 wide; opisthosoma 3.26 long, 2.14 wide. Prosoma deep yellow. Eye sizes and interdistances: AME 0.15, ALE 0.18, PME 0.15, PLE 0.15. AME–AME 0.13, AME–ALE 0.15, PME–PME 0.23, PME–PLE 0.33, ALE–PLE 0.08. MOA 0.48 long, front width 0.38, back width 0.50. Clypeus height 0.23. Chelicerae red brown, with 4 promarginal and three retromarginal teeth. Endites and labium yellow. Sternum yellowish. Leg measurements: I 16.52 (4.28, 5.51, 4.69, 2.04), II 11.94 (3.37, 4.08, 3.06, 1.43), III 9.28 (2.75, 2.96, 2.45, 1.12), IV 11.72 (3.26, 3.98, 3.26, 1.22). Leg

formula: 1243. Opisthosoma yellowish, with many black irregular markings, a pair of yellow longitudinal markings and four indistinct yellowish chevron-like markings. Palpal tibia with a dorso-lateral RTA. Interior branch of DTA wide, with an obvious groove prolaterally. Exterior branch of DTA small, blunt, and slightly depressed prolaterally. Apex of embolus thin and curved ventrally. Conductor membranous and doubled. Median apophysis relatively short, with an acute tip and an inflated base. Apex of tegular apophysis wide and flat (Figs. 38–40).

Female: total length 8.87–11.53. A female (one of paratypes) total length 11.53: prosoma 5.30 long, 3.67 wide; opisthosoma 6.53 long, 4.39 wide. Eye sizes and interdistances: AME 0.23, ALE 0.23, PME 0.18, PLE 0.20. AME–AME 0.18, AME–ALE 0.35, PME–PME 0.43, PME–PLE 0.63, ALE–PLE 0.13. MOA 0.83 long, front width 0.60, back width 0.78. Clypeus height 0.40. Leg measurements: I 13.88 (4.08, 4.49, 3.47, 1.84), II 11.83 (3.57, 4.08, 2.75, 1.43), III 10.10 (3.06, 3.57, 2.35, 1.12), IV 12.55 (3.57, 4.49, 3.16, 1.33). Leg formula: 1423. Epigynum (Figs. 36, 37) with the long median lobe and a pair of blunt epigynal teeth. Copulatory ducts curved anteriorly. Spermathecae ball-like.

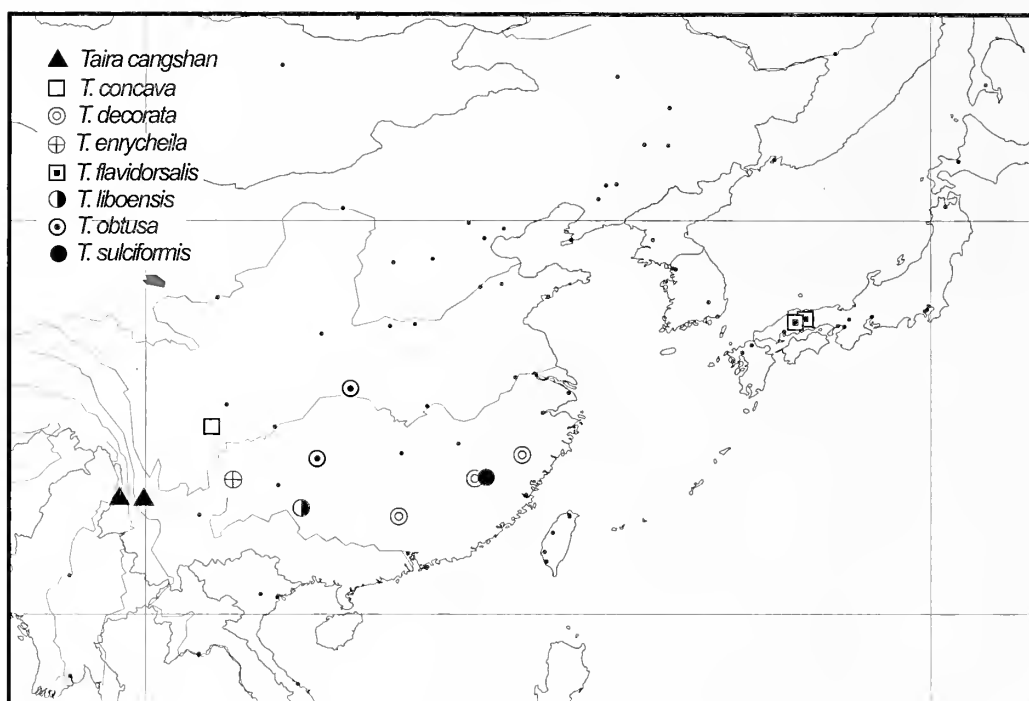


Figure 41.—Distribution of eight *Taira* species.

Distribution.—*Taira sulciformis* has been found in China (Fujian) (Fig. 41).

ACKNOWLEDGMENTS

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Subtle pedipalp dimorphism: a reliable method for sexing juvenile spiders

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Abstract. Quantifying primary sex ratios is necessary for studies in a wide range of areas including adaptive sex ratio modification, population demography, and sex-biased developmental mortality. Adult and penultimate male spiders are easy to sex, due to the great thickening of the male pedipalps, which are used for delivering sperm to the female reproductive tract. However, in many spider species, males and females are apparently monomorphic at hatching, are difficult to rear, and cannibalize their siblings, making assessment of primary sex ratios problematic. One technique for sexing spiders is karyotyping, but this can be challenging and time-consuming, particularly for species with high fecundity, and often requires destructive sampling. Here we report that, although apparently monomorphic, early-instar juveniles of two species of black widow spiders (*Latrodectus hasselti* Thorell 1870 and *Latrodectus hesperus* Chamberlin & Ivie 1935) can be sexed reliably. Palp width measurements are significantly different for males and females at the 3rd instar, with the palpi of juvenile females thinner than those of males. Moreover, sex identification with 89–100% accuracy can be achieved by an experienced observer visually inspecting the palpi of 3rd instar spiderlings under a dissecting microscope. Our results suggest that minimal investment in a pilot study can yield an accurate method for sexing juvenile spiders in the laboratory or field. The suitability of this method should be examined in other species with apparently monomorphic spiderlings, particularly those in which adult males have significantly enlarged palpi.

Keywords: *Latrodectus*, black widow spiders, monomorphic spiders, sexual dimorphism, sex identification

Assessing primary sex ratios, or sex ratios of juveniles observed in the field, is desirable for study in a variety of areas (e.g., adaptive sex ratio modification, population phenology, population dynamics and development of sex-specific growth patterns or behavior). For example, adaptive sex ratio modification has been demonstrated in a variety of species (Austad & Sunquist 1986; Emlen 1997; Nager et al. 1999; Cameron et al. 1999; West & Sheldon 2002; West et al. 2002), including social spiders (e.g., Aviles & Maddison 1991). However in non-social species, there is continued speculation about the possible importance of sex ratio modification since this has only been demonstrated in one non-social species, *Pityohyphantes phryganeus* (C.L. Koch 1836) (Gunnarsson & Andersson 1992; Uhl & Gunnarsson 2001).

Primary sex ratios (ratio of male:female at hatching) are difficult to determine in many spiders in which males and females are apparently monomorphic at hatching (Foelix 1996). Karyotyping has been used to determine sex ratios of fertilized eggs (Aviles & Maddison 1991), and this eliminates the need to rear spiders to later instars. However, this method does not work for all species (Watt, Hasenkampf & Andrade, unpublished), may not be practical for field studies, requires destructive sampling of eggs, and may be prohibitively time-consuming for species with high fecundity. Rearing spiderlings to advanced instars or adulthood to assess sex is problematic because there may be variable success in rearing juveniles due to challenging diet requirements and sibling cannibalism. Even in species that show pronounced sexual dimorphism as adults, juveniles may be apparently monomorphic to the naked eye until later instars when male and female body shape or size diverge significantly and the male's palpi thicken dramatically

in the penultimate instar (Kaston 1970; Mahmoudi, Jovovic, Andrade & Brandt, unpublished). Nonetheless, a number of authors have noted that the pedipalps of males thicken gradually over several instars prior to the penultimate instar (e.g., *Latrodectus* - Bhatnagar & Rempel 1962; *Cyrtophora* - Berry 1987).

Our study describes a method of assessing spiderling sex using the relative size of the palpi in early-instar spiders of two species of black widows (*Latrodectus hasselti* Thorell 1870 and *Latrodectus hesperus* Chamberlin & Ivie 1935). In this genus, males and females appear to be monomorphic at hatching, although they show extreme reversed sexual size dimorphism at adulthood (Kaston 1970). Initial studies of development in *L. hesperus* by one of us (Y. Brandt) suggested there might be differences in the dimensions of pedipalps of males and females very early in development. The objective of this study was to determine whether early sex differences in palp dimensions could provide a simple, non-destructive, morphology-based method for sexing spiderlings. We examined early-instar spiderlings of both species and predicted their sex based on visual inspection and measurement of pedipalp width. We then reared spiderlings to adulthood and report this method yields 94% accuracy or better in determining the sex of 3rd instar spiderlings.

METHODS

Spiders for this study were acquired from outbred populations of redback spiders (*Latrodectus hasselti*) and western black widow spiders (*L. hesperus*), that originated from field-mated, adult females collected in New South Wales, Australia (2002) and San Diego, California (2007), respectively. Voucher specimens have been deposited in the Entomology collection of the Royal Ontario Museum (*L. hasselti*: ROMEnt 112065 through 112067; *L. hesperus*: ROMEnt 112068 through 112070). Egg sacs (*L. hasselti*, $n = 4$ sacs; *L.*

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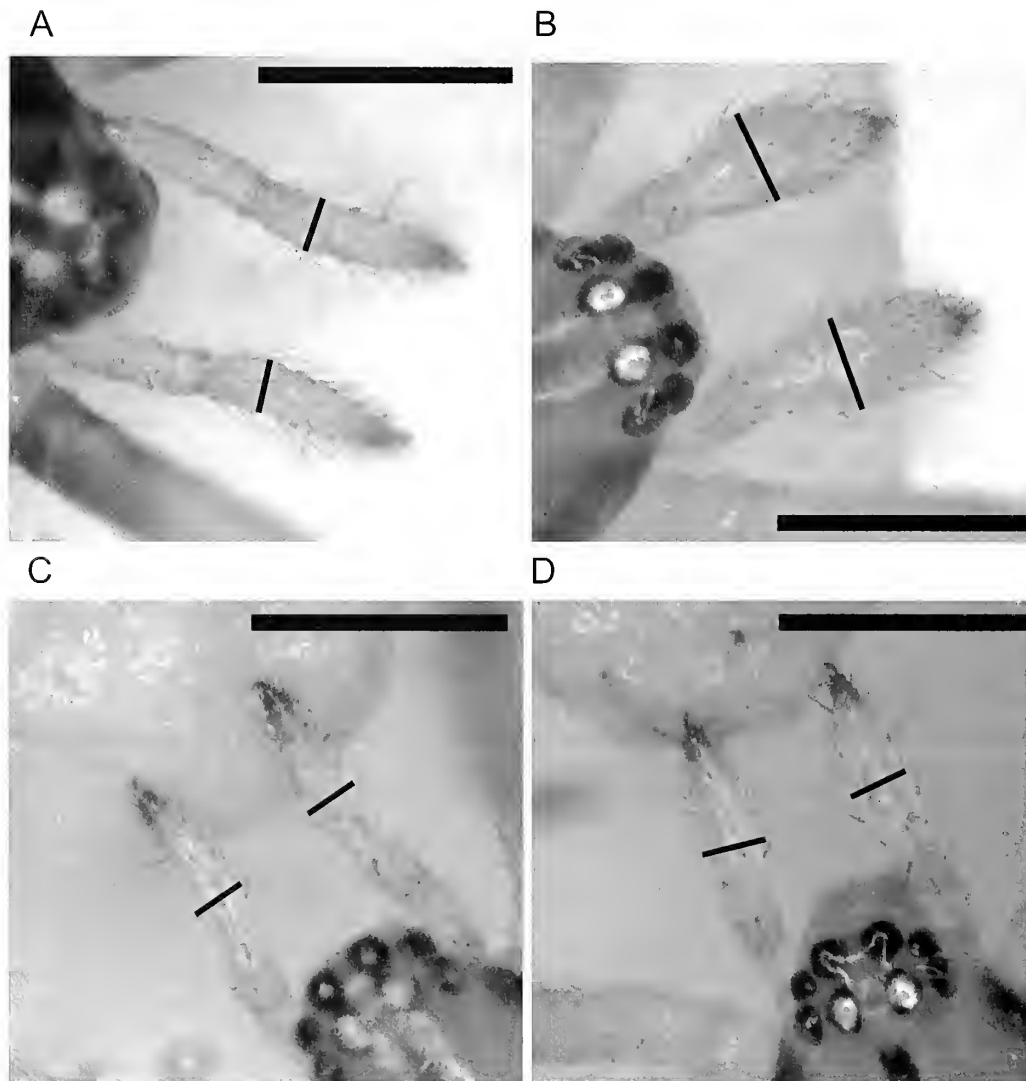


Figure 1.—Digital photographs of dorsal view of portion of the cephalothorax and pedipalps of spiderlings of *L. hasselti* (4th instar female [A] and male [B]) and *L. hesperus* (3rd instar female [C] and male [D]) showing location of measurement of palpal tibia width (black line). Scale bars are 0.50 mm.

hesperus, $n = 2$ sacs) were removed from females' cages shortly after production. Each egg sac was cut open, 40–75 unhatched eggs were randomly chosen and each egg was transferred into an individual clear plastic cage measuring $2.3 \times 3.0 \times 2.3$ cm (Amac Plastic Products Ltd). Eggs and spiders were kept in a controlled-environment room at $25 \pm 5^\circ$ C, 12 hr light : 12 hr dark cycle throughout the study.

Cages were examined every other day, and hatch dates and molt dates were noted. Normally, 1st instar spiderlings remain inside the egg sac and survive on yolk reserves until they molt, emerge from the sac, and begin to take prey (Foelix 1996). Beginning at the 2nd instar, the spiders were fed 1–2 small, wingless fruit flies (*Drosophila melanogaster*) three times each week. The number of fruit flies each spider received was gradually increased as the spider developed. After each molt, approximately 2 more fruit flies were added to each feeding. By the 4th instar, both males and females began receiving larger, heavy-bodied fruit flies (*D. hydei*) three times each week.

Preliminary work suggested that pedipalps of juvenile males might be wider than those of juvenile females, particularly at

the palpal tibia (Jovovic, Brandt & Andrade, unpublished; e.g., Fig. 1A, B). To test whether the appearance of the palps reliably indicated sex differences, an experienced observer examined the pedipalps of each spiderling under a dissecting microscope or examined photographs of the palpi and predicted its sex based on overall pedipalp girth (*L. hasselti*: N. Mahmoudi; *L. hesperus*: M. Modanu). To determine the accuracy of these predictions, all spiders were reared until the 5th (*L. hasselti*) or 6th instar (*L. hesperus*), at which time males and females can be reliably distinguished by the development of notable swellings of the pedipalp in penultimate instar males (Bhatnagar & Rempel 1962; Kaston 1970).

For the visual examination predictions, intact spiderlings were placed under a dissecting microscope (Zeiss Stemi 2000C) and examined, or photographs were taken of their palps (see below). Palps were scored categorically as thick (male-like) or thin (female-like). For *L. hasselti*, sex was determined from 1 ($n = 30$) or 3 ($n = 58$) independent viewings of individuals at the 3rd instar. For *L. hesperus*, there were 3 independent viewings of individuals at the 2nd instar, then 3 independent

Table 1.—Accuracy of sex identification based on visual examination of palpal tibia width of spiderlings for two species of *Latrodectus* spiders. *Null expectation = 50% accuracy; [§]two-tailed test, $df = 1$ with Yates' correction.

Species	Instar	# Correct	# Incorrect	% accuracy	χ^2 *	P [§]
<i>L. hesperus</i>	2 nd	83	52	61.5%	3.143	0.0762
<i>L. hesperus</i>	3 rd	94	6	94.0%	45.858	< 0.0001
<i>L. hasselti</i>	3 rd	78	10	88.6%	29.093	< 0.0001

viewings of photographs of the spider's palps at the 3rd instar. Spiderlings were predicted to be males or females as a function of the majority of the independent assessments.

We determined whether palp width was sexually dimorphic in juveniles by comparing palpal tibia widths. Palps were measured in photographs taken at the 3rd instar (*L. hesperus*) or 4th instar (*L. hasselti*) using a high-resolution digital camera (Nikon DXM 1200) attached to a dissecting microscope. Each spider was anaesthetized by brief exposure to CO₂ and then laid flat on the abdomen. A small sheet of paper was placed under their pedipalps and this was briefly elevated to extend the pedipalps horizontally for photographing. The width of the tibia at the point of connection to the tarsus was measured for each palp using Image Tool (version 3.0, Fig. 1). In *L. hasselti*, maximum prosoma width of a subset of 4th instar spiderlings was also measured and relative palp width (palp width / prosoma width) calculated as this relative measure could allow more accurate predictions.

Analysis.—For each species and instar, we compared accuracy of the categorical assignment method to an expected null of 50% correct using χ^2 analysis (with Yates' correction). We examined whether or not absolute or relative palp width is dimorphic using t -tests (with unequal variances if Levene's test showed a significant difference in variance). We also determined the extent to which absolute or relative palp dimensions reliably predict sex using a logistic regression model with confirmed sex as the dependent variable and relative or absolute palp width as the predictor. t -tests and logistic analyses were completed in SPSS (version 13.0) and χ^2 in GraphPad (<http://www.graphpad.com/quickcalcs/contingency1.cfm>). Sample sizes vary because in some cases isolated eggs did not hatch, or photographs of spiderlings were of insufficient quality to accurately measure body dimensions.

RESULTS

Visual examination method.—Visual examination of palps yielded accurate sex identification in a high proportion of cases (Table 1), with no difference in accuracy between the two *Latrodectus* species ($\chi^2 = 1.109$, $df = 1$, $P = 0.2923$). When palps were visually examined at the 3rd instar, approximately 89% ($n = 88$) of the predictions made for *L. hasselti* and 94% ($n = 100$) of the predictions for *L. hesperus* were accurate (Table 1). Accuracy decreased significantly and prediction was no better than chance if spiderling sex was predicted based on direct examination of spiderlings at the 2nd instar (*L. hesperus*, 62% accuracy, Table 1).

Since the highest accuracy was achieved through visual inspection at the 3rd instar, we focused on understanding sources of error in these predictions. Prediction errors ($n = 6$) for *L. hesperus* spiders categorized at the 3rd instar were all cases of spiderlings initially predicted to be female that were in fact male. Most errors (5/6) occurred for spiderlings in which

the 3 independent predictions were in disagreement. Although in 16 such equivocal cases, the majority categorization was correct, in 24% of these cases (5/21), 2/3 viewings suggested "female-like" palps, but spiders were in fact male. The one additional error occurred when 3/3 viewings suggested "female-like" palps (but the spider was male). We examined our error rate if we excluded from the data set all equivocal cases where the majority categorization was "female-like" ($n = 7$ cases, in two of which this was the correct categorization). In this reduced data set, accuracy increases to 99% (92/93) for sexing by visual examination in *L. hesperus* (although this is not a significant improvement in accuracy, $\chi^2 = 2.083$, $df = 1$, $P = 0.1490$).

Similarly, for 3rd instar *L. hasselti*, 90% (9/10) of prediction errors occurred when individuals considered to have "female-like" palps as spiderlings were actually male. For those *L. hasselti* spiderlings that were examined 3 times ($n = 58$), there were a total of 9 prediction errors (84% correct). In these data, there were 24 equivocal cases (1 of the 3 assessments inconsistent with the others), and in 8 (33%) of these cases, predictions were incorrect. We again examined our error rate if we excluded from the data set all equivocal cases where the majority categorization was "female-like" ($n = 12$ cases, in 5 of which this was the correct categorization). In this reduced data set for *L. hasselti*, accuracy of the visual examination method increases to 96% (44/46 correct, not a significant improvement in accuracy: $\chi^2 = 2.306$, $df = 1$, $P = 0.1289$).

Finally, for 3rd instar spiders, we examined the level of accuracy that could be achieved if only a single visual examination was used to identify sex, as this may be required in some field studies. For *L. hasselti* spiderlings examined independently 3 times ($n = 58$), accuracy was 76% at the first and second assessments, and increased to 86% in the third assessment. Accuracy was 97% for an additional 30 *L. hasselti* spiderlings that were assessed only once. For *L. hesperus* ($n = 100$), accuracy increased from 79% at the first examination, to 94% at the second and finally 98% at the third examination. In both species, accuracy of identification increased with each subsequent (blind) attempt at categorization. As was the case for categorizations based on the consensus of 3 rankings, most of the errors were spiders predicted to be "female-like" that were actually male (29/36 errors for *L. hasselti*, 27/29 errors for *L. hesperus*).

Pedipalp measurement method.—Absolute pedipalp width at the tibia-tarsal joint was sexually dimorphic in spiderlings of both species (Table 2, Fig. 2). Males had significantly wider pedipalps than females at the 3rd instar in *L. hesperus* ($t = -15.847$, $df = 82.504$, $P < 0.001$, Fig. 2A) and at the 4th instar in *L. hasselti* ($t = 14.00$, $df = 23$, $P < 0.001$, Fig. 2B). For *L. hesperus*, absolute pedipalp width accurately predicts the sex of 94.6% of 3rd instar spiderlings (logistic model $\chi^2 = 79.04$, $P < 0.001$). Similarly, absolute palp width accurately predicts

Table 2.—Mean absolute and relative palpal tibia dimensions \pm S.D. for juvenile males and females of two species of *Latrodectus* spiders. *palpal tibia width/ prosoma width.

Species	Instar	Absolute width (mm)		Relative width*	
		Male (n)	Female (n)	Male (n)	Female (n)
<i>L. hesperus</i>	3 rd	0.128 \pm 0.013 (68)	0.097 \pm 0.006 (24)	—	—
<i>L. hasselti</i>	4 th	0.180 \pm 0.006 (6)	0.111 \pm 0.002 (19)	0.225 \pm 0.014 (6)	0.119 \pm 0.003 (15)

the sex of 100% of 4th instar *L. hasselti* ($n = 25$, logistic model $\chi^2 = 27.554$, $df = 1$, $P < 0.001$).

Relative palp width (palp width/prosoma width, $n = 25$ *L. hasselti* spiderlings) was also sexually dimorphic ($t = 7.438$, $df = 5.571$, $P < 0.001$, Table 2, Fig. 2C), and yielded 100% accuracy in predicting sex of 4th instar *L. hasselti* spiderlings ($n = 25$, model $\chi^2 = 27.554$, $df = 1$, $P < 0.001$).

DISCUSSION

We have shown that, in *Latrodectus hasselti* and *Latrodectus hesperus* juveniles, the palpal tibia is significantly wider in males than in females, and this allows accurate identification of sex using a simple visual examination of the spiderlings. In both species, accuracy of over 89% can be attained, and this may increase to 99% if the relatively rare individuals (7/100 for *L. hesperus*, 12/58 for *L. hasselti*) for which equivocal categorization predicts "female-like" palps are excluded (i.e., 3 independent predictions not in agreement, and the majority of predictions suggest "female"). In *L. hesperus*, categorization of spiderlings based on visual examination of palps was incorrect in only 6/100 (6%) of cases. This relatively low error rate could be accommodated statistically in studies of population dynamics or sex ratio, particularly since the polarity of these errors was always males mis-categorized as females. There are a number of alternatives that could increase the accuracy of sexing. First, individuals with equivocal predictions may be reared through one or two additional molts until swelling of male palpi is more readily observable, thus providing highly accurate data with a much-reduced need for labor-intensive rearing than is possible without this technique. Second, repeated scoring of the same individuals may increase reliability. Third, the person scoring the spiders could examine a large number of spiders before attempting categorization. In our study, accuracy of the visual identification method increased with each subsequent attempt at categorization within each species, (i.e., from 76% to 97% in *L. hasselti* and from 79% to 98% in *L. hesperus*). Presumably, this was due to the increased experience of each investigator with each independent examination of the specimens (note that each species was scored by a different researcher, see methods). Fourth, since most of the ambiguous individuals are cryptic males, these individuals may be scored as males, regardless of whether they were scored more frequently as male-like or as female-like, with a relatively small increase in error rate.

Although the polarity of errors for *L. hasselti* was similarly consistent, the proportion of cases with equivocal categorization was far higher (41% of 58 cases). This would be more difficult to accommodate statistically, and would require labor-intensive rearing of almost half of the spiders examined for direct assessment. The higher proportion of equivocal

cases for *L. hasselti* may arise because the use of direct observation of individuals is inferior to examination of photographs for assessment of sex. It is likely that the difference in the number of equivocal cases arises from observer error driven by the method of observation because, if anything, palpi are more dimorphic in *L. hasselti* than *L. hesperus* (Figs. 1, 2), but our predictions were more accurate for *L. hesperus* (Table 1). We note however, that the accuracy of categorization derived from a single examination can be very high after the observer has experience using this technique (i.e., for *L. hasselti*, accuracy = 97% for $n = 30$ spiderlings examined only once).

Our logistic analyses showed that a regression model using measurements of absolute or relative pedipalp width as a predictor could similarly yield up to 100% accuracy in assessing spiderling sex. While this method did not significantly improve accuracy over the visual categorization method it may widen the range of instars and situations in which this technique may be applied.

The practical application of this morphology-based technique to other species will depend on whether or not similar early sexual dimorphism in palp width exists. This may be particularly useful in species that are monomorphic to the naked eye at hatching but in which the male's palpi are notably enlarged at adulthood, as in the genus *Latrodectus*. If palp dimorphism generally develops gradually over several instars, then perhaps the best candidates for sexing spiders visually at an early instar are those species in which males attain sexual maturity in few instars. Applying this method to other species would critically require pilot studies in which individuals are reared until males and females are clearly distinguishable to confirm the applicability of this technique. Early indications that such studies may be fruitful would include significant bimodal clustering of absolute or relative pedipalp width measurements in early-instar spiderlings (e.g., Fig. 2). Such pilot studies should also identify the earliest instars at which this technique would work. In our data set for example, predictions were no better than chance for 2nd instar spiderlings, but highly accurate for spiderlings one instar later (Table 1).

Once pilot studies are complete, the more simple visual examination method can potentially be used for a range of studies. In addition to non-destructive sampling, one advantage of this method is that an experienced observer should be able to classify the sex of juvenile spiders without the disturbance involved in collecting or measuring body parts. Clearly, this method should be very useful for laboratory studies. In addition, for larger species it may be possible to use macro-photography, a portable microscope, or visual inspection using a hand lens in the field to determine sex. One limitation of the visual examination method is that it requires

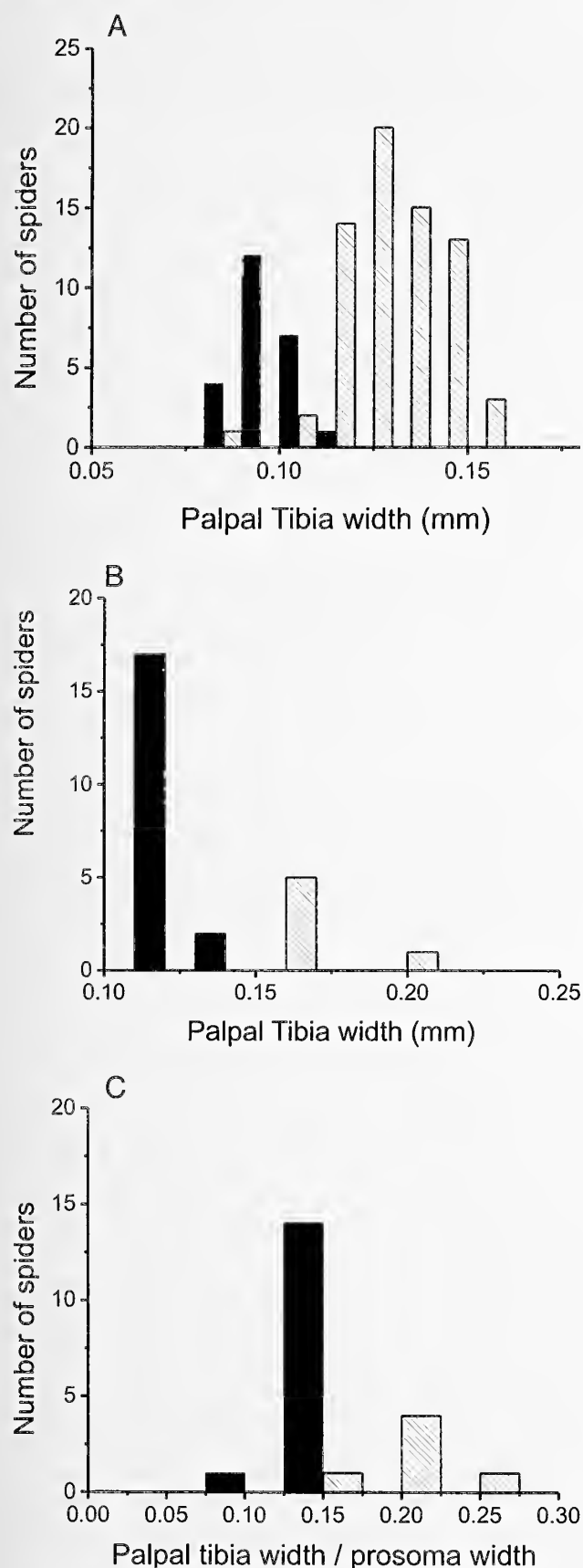


Figure 2.—Distribution of absolute dimensions of palpal tibia of male (cross-hatched bars) and female (black bars) spiderlings of (A) *L. hesperus* (3rd instar), (B) *L. hasselti* (4th instar) and (C) distribution of relative palp dimensions (palpal tibia width/ prosoma width) for 4th instar *L. hasselti*.

knowledge of spider instar, or at least that the spiders under consideration are in the same instar. In the field this may pose difficulties for multivoltine species unless populations are part of long-term monitoring studies. This problem will likely be greatly reduced if measures of relative pedipalp width are used, but confirming this requires additional study.

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Activity pattern of the Neotropical harvestman *Neosadocus maximus* (Opiliones, Gonyleptidae): sexual and temporal variations

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Abstract. We investigated the activity pattern of males and females of the neotropical harvestman *Neosadocus maximus* Giltay 1928 focusing on behavioral variations between day and night and also between summer and winter. Our study also proposes a new method for quantifying arthropod behavior in captivity based on totally random samplings, which minimizes problems of pseudoreplication, so common in studies of behavioral repertoires. Eighteen individuals (nine males and nine females) collected at the Parque Estadual Intervales, São Paulo state, Brazil, were maintained in the laboratory from June 2003 to February 2004 for qualitative and quantitative observations. Thirty-four behavioral acts grouped in five behavioral categories were recorded, with “resting” (53.1%) and “exploration” (30.8%) being the most frequent. The behavioral repertoire of males (32 acts) was more diversified than that of females (29 acts). Moreover, there was a significant effect of sex (male \times female) on the frequency of the behavioral categories: females expended more time resting than did males, whereas males expended more time in exploration and grooming activities than did females. There was also a significant effect of time of day (day \times night) and of season (winter \times summer) on the frequency of the behavioral categories: individuals were most active at night and during summer. Finally, temperature, but not humidity, had a positive effect on the activity of the individuals. In conclusion, the activity of *N. maximus* has sexual, daily, and seasonal variations, which are both quantitative and qualitative.

Keywords: Behavioral sampling, behavioral repertoire, ethogram, rhythm, seasonality, Zeitgeber

Arachnids are generally considered to be primarily nocturnal, although there are exceptions among representatives of the orders Araneae, Solifugae, and Opiliones (Cloudsley-Thompson 1978; Foelix 1996; Punzo 1998; Hoenen & Gnaspini 1999). However, the activity patterns of few arachnids have been quantitatively addressed so that studies on spiders roughly divide the species into day- or night-active (e.g., Marc 1990; Alderweireldt 1994). Additionally, quantitative data on sexual and temporal variations in the activity patterns of arachnids have rarely been reported. Among scorpions, for instance, the seasonal surface activity of mature males differs markedly from that of females in many species (Warburg & Polis 1990). At least for some North American scorpions, females are more active in spring and fall, which is coincident with the peak of insect abundance, whereas males are more active on the surface during midsummer, corresponding to the period of greatest abundance of virgin females (Polis & Farley 1979a, b; Polis 1980).

Most harvestmen species seem to concentrate their activity at night, when temperature decreases and relative air humidity increases (Todd 1949). Certain species, however, are more active during daytime, and others may be found active throughout the day (Bishop 1950; Pfeifer 1956; Williams 1962; Hoenen & Gnaspini 1999). The literature on rhythms is scarce for harvestmen, but includes some information on sexual differences in the activity patterns. Gnaspini (1996), for instance, described that ovigerous females of the Brazilian cavernicolous harvestman *Goniosoma spelaeum* Mello-Leitão 1922 (Gonyleptidae, Goniosomatinae) leave the cave to forage more frequently than males. Recently, the behavioral reper-

tory of males and females has been compared quantitatively in two gonyleptid harvestmen from Brazil, namely *Discocyrtus oliverioi* Soares 1945 (Pachylinae) and *Mischonyx cuspidatus* Roewer 1913 (Gonyleptinae). In both species females fed more frequently than males, whereas males were involved in social interactions more frequently than females (Elpino-Campos et al. 2001; Pereira et al. 2004). Although these two studies describe the daily activity pattern of the harvestmen, they do not provide data on seasonal variation in the frequency of the behavioral categories because both were done only during the summer (December to February).

The great majority of the information regarding seasonal variations in harvestmen is related to the phenology of the species (e.g., Phillipson 1959; Friebe & Adis 1983; Martens 1993; Tsurusaki 2003). These phenological studies provide data on the occurrence of different instars throughout the year, but generally do not deal with seasonal differences in behavior. However, examples of seasonal changes in behavior may be found in the neotropical harvestmen *Acutisoma longipes* Roewer 1913 and *Goniosoma albiscriptum* Mello-Leitão 1932 (Gonyleptidae, Goniosomatinae), which form aggregations inside caves only during the dry and cold season (Machado et al. 2000; Willemart & Gnaspini 2004a) and reproduce only during the wet and warm season (Machado & Oliveira 1998; Willemart & Gnaspini 2004b). The most comprehensive study on seasonal changes in harvestman behavior has been conducted by Gnaspini et al. (2003) with *G. spelaeum*. The authors showed that exits of individuals from the cave were related to sunset time, occurring earlier in winter (June/July) than in summer (December/January). However, the advancement in the time during which individuals leave the cave in summer does not exactly follow

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the advancement in the time of sunset in comparison to winter data, suggesting a change in the phase angle.

Ethograms are important starting points for ethological research and for understanding the biology and ecology of a wide range of animals (Lehner 1996). This methodology allows qualitative and quantitative comparisons between the behavioral repertoires of different species, as well as individuals of the same species belonging to different sexes. In this study we used such an approach to compare the behavioral repertoire of males and females of the neotropical harvestman *Neosadocus maximus* Giltay 1928 (Gonyleptidae, Gonyleptinae), a species commonly found in forest fragments of the Atlantic Forest in southeastern Brazil. Additionally, we investigated for the first time whether the activity pattern of males and females varies between day and night, and also between summer and winter. Our study also proposes a new method for quantifying arthropod behavior in captivity based on totally random samplings, which minimizes problems of pseudoreplication, so common in studies of behavioral repertoires.

METHODS

Taxonomic note.—The genus *Neosadocus* is defined by a cluster of tubercles on the dorso-basal portion of femur IV of males (A.B. Kury pers. comm.), and includes species separated by subtle variations (Kury 2003). Misidentifications are commonplace in the literature and the species treated in this study as *Neosadocus maximus* has been previously named *N. variabilis* by Gnaspini (1996), Machado & Pizo (2000), and Willemart (2002) or *Neosadocus* sp. (Willemart et al. 2007). Two other studies (Willemart & Gnaspini 2003; Castanho & Pinto-da-Rocha 2005), however, properly identified the species as *N. maximus*. The species studied by Machado & Vital (2001) and identified as *Neosadocus* aff. *variabilis* is probably closely related to *N. maximus*, but it is a distinct taxon. Voucher specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP, Brazil).

Collection and rearing.—Individuals of *N. maximus* were collected in a dense Atlantic Forest fragment at the Parque Estadual Intervales (24°14'S; 48°04'W; 800 m elev.), close to the municipality of Ribeirão Grande, southern São Paulo state, Brazil. The annual rainfall in the region ranges from 2,000 to 3,000 mm and the mean annual temperature ranges from 12° C to 20° C. The climate is seasonal with two well-defined seasons. The dry and cold season (hereafter called winter) lasts from April to September, has a mean monthly rainfall of 139 mm, mean monthly air temperature of 17.4° C, and mean monthly air humidity of 79% (data taken *in loco* during 5 yr, 1998–2002). The rainy and warm season (hereafter called summer) lasts from October to March, has a mean monthly rainfall of 306 mm, mean monthly air temperature of 20.9° C, and mean monthly air humidity of 83% (data taken *in loco* during 5 yr, 1998–2002).

Behavioral observations were done in the laboratory based on 18 specimens: nine females and nine males. Each individual received a number from 1 to 18 marked on their dorsal scute with synthetic enamel paint for model airplanes (cf. Elpino-Campos et al. 2001). Individuals were maintained in a communal terrarium (40 × 90 cm base, 20 cm height) containing soil, two individuals of an aroid plant, and pieces

of rotting logs where they could rest and find protection from light. They were fed pieces of dead cockroaches three times a week and always received additional food before the behavioral samplings. From April to September the conditions in the laboratory were (mean ± SD): temperature of 22.1 ± 2.0° C, humidity of 75.6 ± 7.1%, and photoperiod of 12L:12D. Between October and March we changed the laboratory conditions in order to simulate natural climatic oscillations in nature: temperature was 25.5 ± 1.2° C, humidity was 82.0 ± 5.4%, and photoperiod was 13L:11D. Although temperature variation in the laboratory was not the same as in the field, the magnitude of the difference between winter and summer was nearly the same, and the air humidity was close to that measured in the study site. Moreover, the laboratory photoperiod, which is the most important Zeitgeber for many organisms (including arthropods, see Aschoff 1960), reproduced the same seasonal variation observed in nature from winter to summer. Thus, we believe that the results obtained in captivity can be generalized to harvestmen under field conditions.

Behavioral sampling.—The ethogram of *N. maximus* was derived from preliminary 18 h of qualitative *ad libitum* observations of captive individuals (Table 1). The behavioral acts recorded during this phase were classified into five major groups of activities or “behavioral categories”: feeding, exploration, self-grooming, resting, and social interactions (Table 2). Quantitative behavioral observations were done in two distinct seasons: winter samples ($n = 24$) were gathered from June to August 2003, and summer samples ($n = 24$) were gathered from December 2003 to February 2004. In this study we used a new sampling procedure that was designed to minimize the problem of pseudoreplication (see Discussion). According to our protocol, each sample consisted of 1 h of observation randomly selected from midnight to 23:00. After a given 1 h period was selected it was excluded from the next assortments. No sample was done with less than 24 h of interval from the previous sample. During each sample, the behavioral acts were recorded at 1 min intervals (“fixed-interval time point sampling” sensu Martin & Bateson 1993). Only one individual was recorded at each 1 min interval, and its identity was based on a list of random numbers ranging from 1 to 18, in which each number corresponded to the mark of one individual. At the end of each sample, 60 behavioral acts were always recorded (one per minute), and each individual was scanned from one to nine times (median of three times, $n = 48$ sections). When a selected individual was not visible in the terrarium, we searched for it by gently raising the pieces of rotting logs. A flashlight with red filter was used for the nocturnal observations (cf. Elpino-Campos et al. 2001).

Statistical analyses.—The data were classified into two periods: winter and summer. Within each of these two categories, they were also classified in day and night samples. Since the photoperiod differed between the two seasons, the number of day samples was 12 in winter and 13 in summer. Finally, the data were classified into males ($n = 9$) and females ($n = 9$). A log-linear analysis was used to test for the effects of the period of the day, season, and sex on the frequency of the behavioral categories. This analysis is based on fitting a hierarchical log-linear model to the cell frequencies so that it is possible to restate the problem of analyzing multi-way

Table 1.—Behavioral acts of the harvestman *Neosadocus maximus* based on 18 h of ad libitum observations of nine males and nine females maintained under laboratory conditions. Behavioral acts marked with an asterisk were modified from Elpino-Campo et al. (2001).

Behavioral acts	Description
Feeding*	To manipulate organic matter using the chelicerae and pedipalps, inserting it into the mouth. This behavior may be accomplished with the body standing on the legs or with the venter in contact with the substrate. When two or more individuals manipulate the same piece of food at the same time, this behavior is classified as "sharing food."
Walkabout carrying food	To walk carrying food with the chelicerae and pedipalps.
Drinking water	To put the mouthparts in direct contact with the water.
Walkabout – legs II up*	To walk with legs II extended sideways or towards the front without touching the substrate.
Walkabout – legs II touching the substrate	To walk with legs II extended sideways or towards the front touching the substrate.
Motionless – legs II down	To stay motionless with legs II extended sideways downward without touching the substrate.
Motionless – legs II up	To stay motionless with legs II extended sideways upward (Fig. 2).
Motionless – legs II back	To stay motionless with legs II extended back and upward.
Motionless – legs II touching the substrate*	To stay motionless with legs II touching the substrate.
Cleaning the pedipalps*	To pass the tip of the pedipalps through the chelicerae and mouthparts.
Leg threading*	Process of cleaning in which each leg is passed through the chelicerae and mouthparts until the end of tarsus is reached.
Cleaning the venter, dorsum, legs III or IV using legs II	Process of indirect cleaning in which legs II are passed on some parts of the body (venter, dorsum, legs III or IV) and are then cleaned, passing them through the chelicerae and mouthparts until the end of tarsus is reached.
Resting*	To remain motionless with legs retracted over the body and with the venter in contact with the substrate (Fig. 1). While resting individuals may be: (1) isolated, at least 3 cm from each other or (2) in groups, at least three individuals at 0–2 cm apart from each other with legs overlapping. Individuals may rest in protected (under rotting logs) or unprotected sites (open areas of the terrarium).
Aggressive posture	To remain motionless with the pedipalps raised toward another individual.
Mutual leg tapping	Occurs when two individuals walk around each other touching themselves with legs I and II. This is a preliminary step of an intra-sexual fight accomplished exclusively by males.
Intertwining legs IV	After mutual leg tapping, the individuals turn their backs to each other and intertwine legs IV. In this position, each male tries to capsize each other promoting a sudden upward movement in which a male brings femur IV close to the body and pinches legs IV of the opponent.
Chasing other individual	Occurs when a male (generally the winner of the fight) runs after his opponent.
Fighting for food*	Any aggression toward another individual possessing food. It involves attack with pedipalps and touching with the first two pairs of legs.
Attacking with the pedipalps	To approach another individual not possessing food and aggressively attack it with the pedipalps.
Touching other individuals*	Physical contact between two individuals established using legs I and/or II, without aggressive posture (see above) by either individual.

frequency tables in terms that are very similar to ANOVA. According to this model, the natural logarithm of the expected cell frequency is written as an additive (linear) function of effects, including first-order effects and higher-order interactions among the categorical variables (Christensen 1997). This statistical procedure is more than just an alternative form of the chi-square test, which is sensitive to the most common violation of their assumptions, i.e., lack of independence between observations (Kramer & Schmidhammer 1992). Its strength lies in that it can be extended to quite complicated contingency tables involving several variables.

A multiple regression was used to test the relationship between temperature and humidity (independent variables) and number of behavioral acts accomplished per hour (dependent variable). Regarding this analysis, it is important to stress the following: (a) there is no significant correlation between the independent variables ($r = 0.139$; $P = 0.346$), so that there is no problem of multicollinearity in the multiple regression; (b) the number of behavioral acts does not include the category "resting" since we were interested in testing the influence of temperature and humidity only on the activity of the individuals; (c) data from both summer and winter were

used, comprising 48 samples. A two-factor ANOVA was performed to test for differences in the number of behavioral acts per hour (excluding "resting") between day and night in both seasons.

RESULTS

General patterns.—The behavioral repertoire of captive individuals of *Neosadocus maximus* comprises 34 behavioral acts (Table 1). No behavioral act directly related to reproduction, such as courtship, copulation, egg-laying, or parental care has been recorded in captivity. During the 48 h of quantitative observations, four acts of the behavioral repertoire were not recorded, all belonging to the category "social interactions" (numbers 27–29 and 31 in Table 2). The most common behavioral categories were "resting" and "exploring," which accounted for 53.1% and 30.8% of the total of observations, respectively (Table 2). Most of the "resting" observations were of individuals grouped underneath rotting logs (Fig. 1), whereas most of the "exploring" observations were of motionless individuals with their second pair of sensorial legs upwards (Table 2; Fig. 2). The great majority of the individuals fed alone, and food sharing was recorded in

Table 2.—Frequency of each behavioral act for captive adults of the harvestman *Neosadocus maximus* in two seasons (winter and summer). In parentheses is the total number of behavioral acts observed for the individuals in each season.

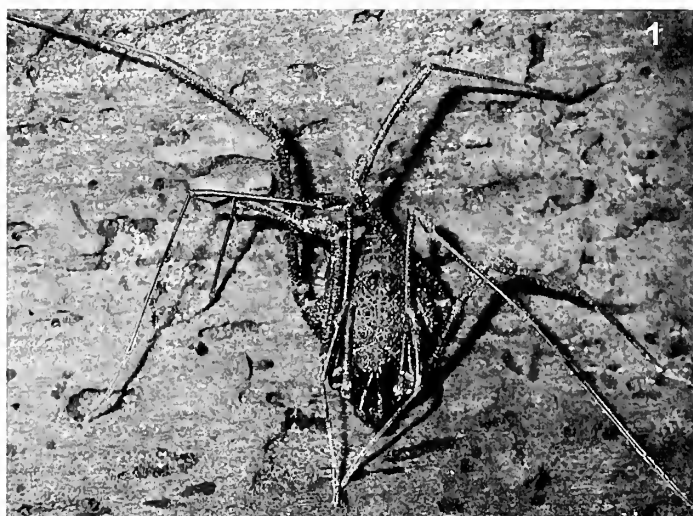
Behavioral acts	Frequency of the behavioral acts (%)					
	Males (n = 9)		Females (n = 9)		Total (n = 18)	
	Winter (697)	Summer (661)	Winter (743)	Summer (779)	Winter (1440)	Summer (1440)
FEEDING	3.73	14.54	3.23	13.99	3.48	14.23
1. With the body erect	3.01	11.5	2.15	9.50	2.57	10.42
2. With the body in contact with the substrate	0.29	1.83	0.82	2.43	0.56	2.15
3. Walkabout carrying the food	0.14	0.61	0.13	1.16	0.14	0.90
4. Food sharing	0	0.15	0	0.51	0	0.35
5. Drinking water	0.29	0.45	0.13	0.39	0.21	0.41
EXPLORATION	34.85	39.94	21.27	28.50	27.85	33.75
6. Walkabout – legs II up	4.3	3.78	2.16	2.18	3.19	2.92
7. Walkabout – legs II touching the substrate	5.16	4.69	4.98	3.34	5.07	3.96
8. Motionless – legs II down	2.73	11.04	2.69	7.32	2.71	9.03
9. Motionless – legs II up	14.20	12.56	7.27	11.04	10.63	11.73
10. Motionless – legs II back	5.45	5.60	1.48	2.95	3.40	4.17
11. Motionless – legs II touching the substrate	3.01	2.27	2.69	1.67	2.85	1.94
SELF-GROOMING	5.90	7.10	3.22	5.26	4.51	6.12
12. Cleaning the pedipalps	2.44	3.93	1.48	2.95	1.94	3.40
13. Leg threading – legs I	1.00	1.66	0.54	1.28	0.76	1.46
14. Leg threading – legs II	1.59	0.45	0.94	0.77	1.25	0.63
15. Leg threading – legs III	0.29	0.61	0.13	0.26	0.21	0.42
16. Cleaning legs III with legs II	0	0.15	0	0	0	0.07
17. Leg threading – legs IV	0.44	0.15	0	0	0.21	0.07
18. Cleaning legs IV with legs II	0.14	0	0	0	0.07	0
19. Cleaning the venter with legs II	0	0.15	0	0	0	0.07
20. Cleaning the dorsum with legs II	0	0	0.13	0	0.07	0
RESTING	53.37	36.91	69.86	50.45	61.87	44.22
21. Resting alone protected	10.90	3.63	8.34	10.53	9.58	7.35
22. Resting alone unprotected	5.16	6.20	3.77	0.90	4.44	3.33
23. Resting in group protected	37.02	27.08	57.07	38.76	47.36	33.40
24. Resting in group unprotected	0.29	0	0.68	0.26	0.49	0.14
SOCIAL INTERACTIONS	2.15	1.51	2.42	1.80	2.29	1.68
25. Aggressive posture	0	0	0	0.13	0	0.07
26. Mutual leg tapping	0.14	0	-	-	0.07	0
27. Intertwining legs IV	0	0	-	-	0	0
28. Chasing another individual	0	0	-	-	0	0
29. Male vs. female fight	0	0	0	0	0	0
30. Fighting for food	0	0.45	0.13	0.13	0.07	0.28
31. Attacking with the pedipalps	0	0	0	0	0	0
32. Male touching male	1.29	1.06	-	-	0.69	0.49
33. Female touching female	-	-	0.81	0.77	0.35	0.42
34. Female touching male, and vice versa	0.72	0	1.48	0.77	1.11	0.42

only 0.3% of the observations (Table 2). Probably as a means to avoid food sharing or even food plundering, some individuals carried the food away before starting consumption. Grooming behavior occurred when the harvestmen were moving around the terrarium and, more frequently, after feeding (when both legs and pedipalps were cleaned) and social interactions, such as fights and mutual leg tapping.

Sexual variation.—The behavioral repertoires of males and females of *N. maximus* differed both qualitatively and quantitatively. The behavioral acts number 26–29 were accomplished exclusively by males and are related to a ritual of intra-sexual aggression (Table 1). Five fights between males were observed in the qualitative observations, but during the

quantitative samplings this behavior was not recorded. A fight starts with two males walking around each other, touching the opponent with the first and the second pairs of legs. After about three to five complete turns the males stop and, if the fight escalates, they turn their backs to each other and intertwine their fourth pairs of heavily-armed legs. In this position, each male moves the femur IV pinching the opponent's leg between the apophysis and spines of their own femur and coxa IV. The fight ends when one of the contenders leaves the place.

The log-linear analysis showed that there was a significant effect of sex (male vs female) on the frequency of the behavioral categories (Table 3). Females were seen resting and interacting with conspecifics more frequently than males



Figures 1, 2.—Adult *Neosadocus maximus*. 1. Female of *N. maximus* resting under a rotting log in captivity. Note that the legs are retracted over the body and the venter is in contact with the substrate. 2. Male of *N. maximus* walking on the vegetation in the field. Note the second pair of sensory legs extended sideways and touching the substrate (photos: B.A. Buzatto).

(Fig. 3). Males, on the other hand, were more active, exploring and grooming more than females (Fig. 3). Individuals of both sexes fed with a similar frequency (Fig. 3). Aggressiveness among males, however, may explain why females rested

Table 3.—Results of the log-linear analysis used to test for the effects of time (day vs night), season (summer vs winter), and sex (male vs female) on the frequency of behavioral categories accomplished by captive individuals of the harvestman *Neosadocus maximus*.

Model	Chi-square	df	P
Season × Time × Sex	1.587	4	0.811
Season × Time	8.175	8	0.417
Time × Sex	0.803	4	0.938
Season × Sex	8.498	12	0.745
Season (summer vs winter)	160.960	8	< 0.001
Time (night vs day)	33.929	8	< 0.001
Sex (male vs female)	76.722	8	< 0.001

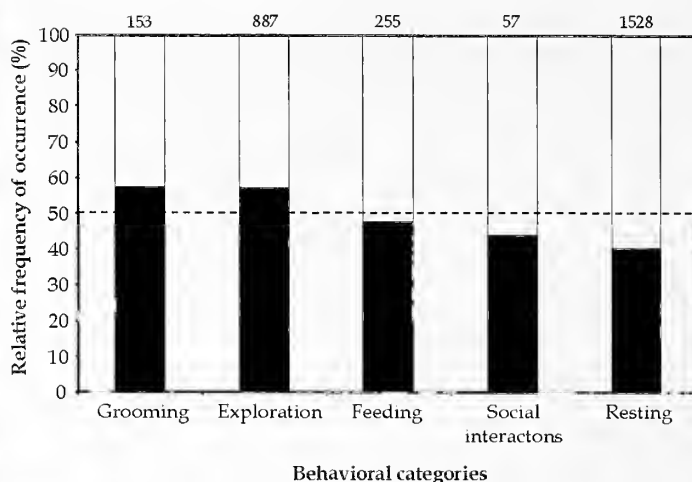


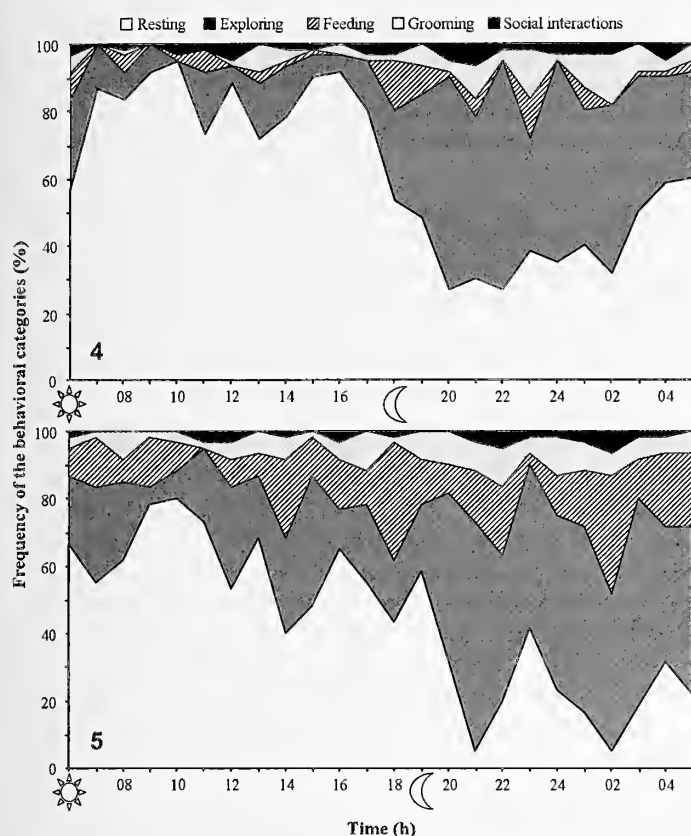
Figure 3.—Comparison of the relative frequency of occurrence of the behavioral categories observed for males (black bars) and females (white bars) of the harvestman *Neosadocus maximus*. The numbers above the bars indicate the total number of records in each behavioral category.

aggregated more frequently than males, both in winter and summer (Table 2).

Temporal variations.—The log-linear analysis showed that there was a significant effect of the period of time (day vs night) on the frequency of the behavioral categories (Table 3). Individuals of *N. maximus* remained inactive during most of the daylight hours, when they were resting underneath rotting logs (Figs. 4, 5). In winter, individuals became active at about 17:00 h, i.e., one hour before dusk (Fig. 4). In summer, activity began at about 19:00 h, just after dusk (Fig. 5). Night activities included exploring the environment by walking around the terrarium and feeding on pieces of dead cockroaches (Figs. 4, 5). Male-male fights were also restricted to the nocturnal period. In winter, activities started to decrease at about 02:00 h, whereas in summer activities started to decrease only at about 05:00 h, when most of the individuals were seen resting or moving to the shelters underneath rotting logs (Figs. 4, 5).

The log-linear analysis also showed that there was an effect of season (winter vs summer) on the frequency of the behavioral categories (Table 3). Even though resting and exploring were the most common activities in both seasons, there was an increase in the frequency of resting from summer to winter, and a decrease in the frequency of exploration from summer to winter (Table 2). Additionally, there was a marked reduction in the frequency of feeding from one season to the other: during winter, in nearly 4% of the observations individuals were feeding versus 14% during summer (Table 2). The frequency of the categories self-grooming and social interactions were similar between seasons (Table 2). It is worthy to note that the interactions between sex and season as well as time and season have no significant effect on the frequency of the behavioral categories (Table 3).

A positive relationship between the number of behavioral acts and the temperature was detected, but this relationship was not significant for humidity (Table 4). The mean number of behavioral acts accomplished per hour during the night was greater than during the day in both seasons ($F_{(1, 44)} = 99.915$;



Figures 4, 5.—Daily activity schedule of the harvestman *Neosadocus maximus* in (4) winter and (5) summer. The moon and the sun indicate dusk and dawn, respectively.

$P < 0.001$; Fig. 6). Additionally, when comparing seasons, the mean number of behavioral acts accomplished per hour was greater in summer than in winter ($F_{(1, 44)} = 25.368$; $P < 0.001$; Fig. 6).

DISCUSSION

Comparisons with other species.—Harvestmen are excellent model organisms for behavioral studies because individuals of many species are abundant in the field and are easily maintained in captivity, where they behave in a similar way to that observed in the field (e.g., Capocasale & Bruno-Trezza 1964; Elpino-Campos et al. 2001; Willemart 2001; Pereira et al. 2004), facilitating quantitative and qualitative comparisons between species. In this study, we used the neotropical harvestman *Neosadocus maximus* in order to investigate sexual and temporal variations in the behavior of captive individuals. The data obtained here may also be compared with those previously obtained for other harvestman species reared under similar conditions. The number of behavioral acts recorded for

Table 4.—Multiple regression between the number of behavioral acts (excluding resting) accomplished by captive individuals of the harvestman *Neosadocus maximus* and two independent variables: temperature and humidity ($F_{(2, 45)} = 4.80$; $P = 0.013$).

Independent variable	b	$F_{(1, 44)}$	P
Humidity	0.066	1.174	0.284
Temperature	0.485	7.425	0.009

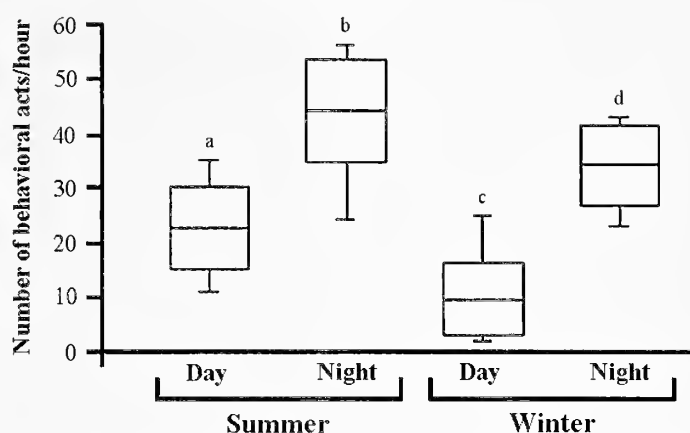


Figure 6.—Comparison of the number of behavioral acts (excluding resting) accomplished per hour by individuals of the harvestman *Neosadocus maximus* during day and night in two seasons (summer and winter). The horizontal lines represent the mean, the boxes represent the standard deviation, and the vertical lines represent the range (minimum and maximum values in each sample). Different letters above the box-plots indicate significant difference with $P < 0.05$.

N. maximus is greater than those recorded for the harvestmen *Discocyrtus oliverioi* (25 acts, Elpino-Campos et al. 2001) and *Mischonyx cuspidatus* (20 acts, Pereira et al. 2004). This difference may be attributed to two main factors: (1) some behavioral acts described in the previous studies were split into two or more different acts in our study (e.g., acts 8–11); (2) *N. maximus*, in fact, presents a number of distinctive behavioral acts that were not recorded before, such as those related to self-grooming (number 16 and 18–20) and social interactions (number 26–28). There was also a marked difference among the three harvestman species in the frequency of the behavioral categories exploration and resting. In *D. oliverioi* and *M. cuspidatus*, exploration was the most common behavioral category, comprising nearly 70% of the observations, whereas in *N. maximus* this category accounted for 28% in winter and 34% in summer. Resting, which ranged from 11 to 17% in *D. oliverioi* and *M. cuspidatus*, was the most frequent behavioral category for *N. maximus* comprising 44 to 62% of the observations. These discrepancies could be related to differences in the sampling methods, since Elpino-Campos et al. (2001) and Pereira et al. (2004) concentrated the quantitative observations at night (when the individuals were more active), whereas in the present study we scattered the behavioral samplings equally throughout the whole day. In fact, if we analyze the data obtained only in the night samples for *N. maximus*, the frequency of resting drops to 22% and of exploration increases to 52%. Therefore, we believe that the data presented in this study are a more realistic scenario of time allocation in harvestmen during the whole day.

Contrary to *D. oliverioi* and *M. cuspidatus*, individuals of *N. maximus* did not copulate or lay eggs in captivity, so that the behavioral category reproduction, which comprised one to seven behavioral acts and accounted for 0.1 to 1.8% of the observations in the previous studies, was not included here. Field observations indicate that *N. maximus* oviposits on the undersurface of leaves and eggs are attended by females (G. Machado unpubl. data). It is possible that the lack of

appropriate oviposition sites in the terrarium have constrained the reproductive activity of the females. Males, on the other hand, accomplished certain behavioral acts, such as intra-sexual aggressions, that are possibly related to territorial defense and reproduction. Male-male fights have already been described for several harvestman species (e.g., Pabst 1953; Parisot 1962; Edgar 1971; Mora 1990; Macías-Ordóñez 2000; Willemart et al. 2006), but this is the first record of this kind of agonistic behavior among gonyleptids. The use of legs IV, which bear large spines and tubercles, shed light on the behavioral roles of the leg armature in *N. maximus* and other gonyleptid harvestmen as well. Until now, the only function attributed to the armature of legs IV in males was to deliver a nipping upon manipulation, which has been interpreted as a defensive behavior against potential predators (Bristowe 1925; Capocasale & Bruno-Trezza 1964; Gnaspini & Cavalheiro 1998; Machado 2002). A more detailed description of the fights and the functional morphology of legs IV in *N. maximus* will be described elsewhere (Willemart et al. unpubl. data).

Sexual and temporal variation.—Males and females of *N. maximus* differed in the relative frequency of the behavioral categories, with males exploring more frequently than females. This result contrasts with those obtained for *D. oliverioi* and *M. cuspidatus*, in which females fed and explored more frequently than males (Elpino-Campos et al. 2001; Pereira et al. 2004). Since both *D. oliverioi* and *M. cuspidatus* reproduced in captivity, the higher frequency of feeding activities in females compared to males was attributed to the accumulation of energy for egg production and maturation (Pereira et al. 2004). The higher frequency of exploration by males compared to females in *N. maximus* may be explained by at least two non-exclusive factors: (1) in this species males seem to be territorial (G. Machado unpubl. data) and thus need to invest time patrolling and exploring their territories; (2) females did not oviposit in captivity and, thus, were not continuously producing eggs, which would reduce the demand for food resources and consequently decrease the frequency of activities related to foraging. Since self-grooming occurs more frequently when individuals are moving around and after feeding (Pereira et al. 2004), the fact that males explored more than females may account for the higher frequency of grooming compared to females.

The daily activity of the individuals of *N. maximus* in captivity was predominantly nocturnal, and light seems to be the most important Zeitgeber promoting synchronization of the activity rhythm. This observation is congruent with data previously obtained in the field, where 100% of the feeding observations in this species occurred at night (Machado & Pizo 2001). The activity pattern, however, presents seasonal variations with a clear change in the phase angle between activity and sunset/sunrise hours from winter to summer. During winter, individuals left the shelters earlier, one hour before dusk. The peak of activity occurred nearly at 20:00 h, and at 02:00 h there was a marked decrease in the frequency of behavioral acts not related to resting. In contrast, during summer, individuals left the shelter only after dusk, remained active throughout the night, and returned to the shelter at about 05:00 h, nearly one hour before the onset of light. In some aspects, this pattern of activity is similar to that described for the cavernicolous harvestman *Goniosoma*

spelaeum, in which the individuals also left the cave earlier in winter when compared to summer (Gnaspini et al. 2003). However, contrary to the present study, individuals of *G. spelaeum* returned later to the shelter during winter. The authors attributed this change in the phase angle to the time available to forage outside the cave, which is shorter during summer. It is possible that captive individuals of *N. maximus* can find food faster than individuals of *G. spelaeum* in the wild and thus can return earlier to their shelters. Another possibility is that different species respond differently to seasonal variations in biotic and abiotic factors. We suggest that future studies investigate how hunger and other physiological constraints modulate long-term changes in the biological rhythms of harvestmen.

In our study we demonstrate that temperature, but not humidity, has a positive relationship with the activity of captive individuals of *N. maximus*, which may explain why the individuals were more active during summer. A similar result has been reported by Capocasale & Bruno-Trezza (1964), who reared individuals of the gonyleptid *Acanthopachylus aculeatus* (Kirby 1818) in the laboratory and showed that foraging activity seems to be directly related to temperature. However, the predominant nocturnal activity of the species in the field and in the laboratory should not be attributed to temperature since the latter decreases at night. We believe that the decrease in light intensity at dusk, rather than the decrease in temperature, controls the beginning of activity in *N. maximus*. After darkness, however, air temperature can be an important abiotic factor determining harvestmen activity; the warmer the night the more active are the individuals. Additionally, it is important to stress the role of phylogeny in determining the activity pattern of harvestmen. *N. maximus* belongs to a clade in which most species are mainly nocturnal. Predominant diurnal activity among gonyleptids seems to be restricted to the clade composed of the subfamilies Progonyleptoidellinae + Caelopyginae (Hoenen & Gnaspini 1999).

Methodological approach.—The density of harvestmen used in our terrarium (18 individuals in 0.36 m²) is certainly much higher than the density in the wild, which is no more than 0.04 individuals/m² (G. Machado unpubl. data). Crowding may increase the frequency of some behavioral acts, mainly those grouped in the behavioral category “social interactions”. However, for the great majority of the behavioral acts (including those grouped in the behavioral categories “feeding,” “exploration,” “self-grooming,” and “resting”) the density of individuals in captivity probably had no evident effect. Moreover, since these last four behavioral categories comprise nearly 98% of the behavioral acts in both seasons, we believe that the results obtained under captive conditions for *N. maximus* provide a realistic scenario of time allocation throughout the day and also in different seasons. The lack of appropriate oviposition sites in our terrarium probably inhibited some behavioral acts, mainly those related to reproduction. We acknowledge this drawback of our laboratory work and recommend that future studies try to reproduce as good as possible the oviposition sites of the study species in the rearing terrarium.

Despite some minor problems mentioned above, harvestmen are very convenient animals to keep in captivity since many species are relatively easy to maintain and may live for several months or even years (Willemart 2007). In our case, to

study animals in the laboratory provided the opportunity to quantify the behavior of a great number of individuals in each sampling section and also made it possible to compare the behavioral schedule of the very same subjects in two seasons, which would be very difficult in the wild. Simulating natural variations in climatic conditions, we showed that there were differences in the frequency of five behavioral categories recorded for *N. maximus*, both at the scale of the day and of the year (winter vs summer). This temporal variation may be endogenously regulated and/or dependent on the environmental variables we manipulated, but we can not actually differentiate between these two possibilities.

In this study we also proposed a new sampling procedure for quantitative ethograms that minimizes problems of pseudoreplication. Traditionally, behavioral samplings in quantitative ethograms are accomplished at regular intervals and all subjects are recorded at each scan. Using this procedure, one will face at least two situations that violate the assumption of independent observations required by many statistical tests, especially the frequently used chi-square (see discussion in Kramer & Schmidhammer 1992): (1) one behavioral act may influence the chance of another behavioral act being accomplished in sequence; (2) if the individual A is interacting with the individual B, this behavioral act will be counted twice because the interaction is reciprocal. Yet the "traditional" ethograms have an advantage: the amount of information in each sampling section is high; more specifically $n \times s$, where n is the number of individuals and s is the number of scans. Using the method proposed here, the amount of data in each sampling section is only s because only one individual is scanned at a time. Sampling one individual per scan, however, is exactly the solution for the situation (2) above. Additionally, the median number of times the same individual was scanned per sampling section along the entire period of our study was three. These repeated samplings on the same individuals were spaced out in time, which attenuates the problem exposed in the situation (1). Finally, we also took care of spreading the sampling sections along the time, spacing them with intervals of at least 24 h in order to attenuate the possible influence the activities accomplished in one day could have on activities accomplished in the following day. This is not a standard procedure in "traditional" ethograms, which concentrate the samplings in the periods of more activity or in fixed times of the day.

We are aware that sampling the same individuals (in our case 18 harvestmen) is, per se, a source of pseudoreplication, but changing each animal for another one after it was sampled does not seem a reasonable procedure in behavioral studies and would demand a huge quantity of animals. Anyone interested in controlling potential differences among individuals may include each one of them as additional factors in the log-linear analysis. Here we avoided this approach because our main goal was to detect general patterns.

Conclusions.—In conclusion, we demonstrated that the activity pattern of the neotropical harvestman *N. maximus*, determined here by the frequency of five behavioral categories, shows sexual and temporal variations. These variations are both quantitative and qualitative since some behavioral acts are restricted to one sex or period of the day. The sampling protocol proposed here should be used in future studies

dealing with behavioral repertoires and ethograms because it minimizes the problems of pseudoreplication and provides a more realistic view of the allocation of time and energy for different activities. The great advantage of this method is that it provides a suitable sampling design that generates independent data, instead of trying to correct the problem of non-independence a posteriori using complicated statistical procedures. Our protocol should be useful as a standard method in behavioral samplings not only for harvestman, but for the study of any arthropod reared in captivity.

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First male sperm precedence in multiply-mated females of the cooperative spider *Anelosimus studiosus* (Araneae, Theridiidae)

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Abstract. Patterns of sperm usage in multiply-mated females have profound fitness consequences for males, and create strong selective pressure on male behavior. In the cooperative theridiid spider *Anelosimus studiosus* Hentz 1850 adult males are tolerated in females' webs, and females have been observed to mate multiply with different males. In this experiment, virgin females were mated with two different males on consecutive days under controlled conditions to determine paternity patterns and behavioral responses of males to non-virgin females. The paternity of broods was analyzed using randomly amplified polymorphic DNA (RAPDs). Fifteen broods were analyzed and complete first male sperm precedence was found. Mating behavior differed between first and second males with the first males attempting fewer intromissions, but having a longer total time of intromission. This suggests that the second males are either prevented from normal copulation, or are reacting to the different condition of the females. The sperm precedence pattern is discussed with respect to its ramifications for male behavior, juvenile inclusive fitness, and the evolution of cooperative behavior.

Keywords: Social spiders, mating behavior, RAPDs, sexual selection

When females mate multiply, sperm precedence patterns can affect the fitness of all individuals involved. For males who have both mated with the same female, the fitness consequences are clear and directly related to the proportion of her brood they have fertilized (Trivers 1972). Because of this, males often compete with each other for access to females, or to be chosen as mates by females (Andersson 1994). Males may also compete for fertilizations after copulation through such avenues as mate guarding or copulatory plugs, the necessity or efficacy of which is affected by sperm precedence (Parker 1984). Patterns of sperm precedence may affect the female's fitness by influencing the genetic variability of her brood, or the proportions of her brood fertilized by males of differing quality. There is also accumulating evidence of females manipulating fertilization patterns of their broods in response to male attributes (Eberhard 1996). Examples of this in spiders include selective sperm storage in response to copulation duration (Bukowski & Christenson 1997a & b), and the fact that, with paired spermathecae, spiders may be pre-adapted for paternity manipulation (Snow & Andrade 2005).

Patterns of sperm precedence will also affect the composition of full and half-sibs within broods of polyandrous females. In social species, the relatedness among brood-mates can have profound effects on their fitness (Hamilton 1964). The relatedness among group members is therefore important for a complete understanding of the selective costs and benefits to group living (for review see Caraco & Giraldeau 1991).

Mating systems are particularly important to the evolution of sociality in spiders. Social spider colonies are generally inbred (Riechert & Roeloffs 1993; Johannesen et al. 2002). In fact, genetic analysis of *Anelosimus eximius* Keyserling 1884 colonies suggests that there is no gene flow at all among colonies (Smith & Hagen 1996). It is likely that the cooperative behaviors and female-biased sex ratios of cooperatively social spider species are maintained by interdemec selection, fostered

by the high levels of relatedness among colony members (Avilés 1997). Isolated local populations of asocial or subsocial spiders will become inbred through genetic drift, which could then promote the evolution of cooperative behaviors. The rate at which a population loses genetic diversity (i.e., the effective population size) is affected by its mating system in that monogamous populations lose diversity faster than promiscuous populations (Parker & Waite 1997). This inbreeding is likely an important factor in the evolutionary transition from subsociality to permanent sociality in spiders (Bilde et al. 2005).

Anelosimus studiosus Hentz 1850 is a relatively small (about 8 mm long) theridiid spider which ranges from Argentina to New England (Agnarsson 2006; Agnarsson et al. 2007). This species is common in the southeastern USA and can be found in extremely high densities along waterways (Jones et al. 2007). This species is described as subsocial (Wilson 1971) and, specifically, "prolonged subsocial" (Rayor & Taylor 2006), in that juveniles and adult males are tolerated in an adult female's web, but other adult females usually are not (Brach 1977; but see Furey 1998; Jones et al. 2007). Previous experiments have demonstrated that, under controlled laboratory conditions, colony prey capture increases with the age and number of juveniles in the colony (though resources per individual decline with colony size), and variation in prey mass decreases with the number of juveniles present (Jones & Parker 2000). Females can produce up to at least three broods over their lives usually with several weeks between broods (Jones, unpubl. data). It has also been shown that in semi-natural conditions, delayed juvenile dispersal benefits juvenile survivorship and development as well as the mother's ability to produce future broods (Jones & Parker 2002). While it is clear that individual juveniles are better off in their natal group than on their own, the exact relationship of individual fitness to group size is not yet known. Whatever this relationship, a juvenile's fitness is likely to be affected by its relatedness to its brood-mates. We have observed that females will mate

multiply if presented with more than one male, so broods may be composed of either full-sibs, or a mixture of full and half-sibs.

Members of the family Theridiidae are "entelegyne" spiders, in that the female reproductive tract has a conduit morphology, with sperm leaving the storage organ to fertilize eggs through a different opening than that into which they were deposited (Foelix 1996). It has been suggested that this morphology will put the first mate's sperm closest to the point of fertilization, and thus lead to first mate sperm precedence (Austad 1984). However, studies of sperm precedence in entelegyne spiders have yielded estimates of proportions of first male from 0.95 to only 0.37 (reviewed by Elgar 1998). In the theridiid Australian redback spider the mean first male precedence was 0.44, but ranged from 0.0 to 1.0 (Andrade 1996). In this study we seek to determine sperm precedence in *A. studiosus* by sequentially pairing females with two males, recording mating behavior, and using the animals' DNA and RAPD analysis to determine parentage.

METHODS

Collection and Rearing.—*Aelosinus studiosus* colonies containing juveniles were collected in southern Louisiana in September of 1999 from bayous in Tickfaw State Park (30°22'N, 90°37'W) and Fontainebleau State Park (30°20'N, 90°02'W). The bayous were accessed by pirogue and the webs were mostly collected from low-hanging cypress branches (voucher specimens are deposited in the Museum of Biological Diversity at The Ohio State University, Columbus, Ohio). We maintained the colonies in plastic containers (18 × 14 × 6 cm) that were laced with sewing thread to provide substrate for web building. The colonies were kept at buffered ambient temperatures (20–28° C) under natural light conditions, were fed *Drosophila melanogaster* and *D. virilis* ad libitum, and misted with distilled water three times a week. We kept the colonies in a greenhouse under natural lighting conditions. In order to ensure the virginity of experimental animals, as the juveniles approached maturity, females were isolated in new containers, and the penultimate males were grouped together (by natal colony) in another set of containers.

Experimental Matings.—Females that had undergone their final molt in isolation were selected for this experiment. Twenty-five females from eight different colonies, but no more than four females from any one colony, were used. We released males from two different colonies (other than the colony of their prospective mate) into a female's container one at a time, on consecutive days. Matings were videotaped with a Sony digital 8 camera for behavioral analysis. The resolution of the video did not allow fine details of palpal insertions, such as the extension of the embolus, to be observed. We estimated copulation as periods when the male's palps were resting stationary against the female's genital opening. The onset of copulation was recorded as when the palp would ease against the genital opening and stop, and the end of copulation was recorded when the male pushed against the female and broke loose with a conspicuous jerk. We quantified the number and timing of copulations and copulation attempts. After mating, the males were frozen for later DNA extraction. Mating usually commenced within a few minutes after the introduction of the males. We removed the males after they had broken

copulation, moved off from the female, and for ten minutes showed no further attempt at copulation. On four occasions the males had not attempted copulation after 15 min. These males were removed from the container and the process was restarted with new males. Abstinent males were not reused. After the females had mated the second time, we returned them to the greenhouse rearing conditions. Females that produced broods were allowed to rear them through the third instar, after which the female and juveniles were frozen for DNA extraction.

DNA Extraction and PCR.—To the 1.5 ml tubes containing the frozen spiders, 200 µl of CTAB and 1.5 µl Proteinase K (100 µg/ml) were added. The spiders were thoroughly ground with a pestle in the tube and incubated at 60° C for 1 h. One extraction with 100 µl of phenol and 100 µl of CIA (24:1 chloroform:isoamyl alcohol), and one extraction with 200 µl of CIA were performed. The samples were ethanol precipitated, resuspended in 100 µl of distilled water, and stored at 4° C. The concentration of the samples was estimated by gel comparison with concentration standards.

Randomly amplified polymorphic DNA (RAPDs) uses single relatively non-specific ten base pair primers (synthesized at OSU) to amplify regions of the genome that contain complementary primer annealing sites. The regions that are amplified are arbitrary but heritable, and therefore, useful (Williams et al. 1990). Under similarly controlled mating conditions, RAPDs were used to assign sperm precedence in a beetle (Carbone & Rivera 2003). The reactants for an individual 14 µl reaction consisted of: 9.9 µl, UV irradiated distilled water; 1.5 µl of 1 µM dNTPs; 1.5 µl reaction buffer (10 mM Tris HCl, pH 8.3; 50 mM KCl; 2 mM MgCl₂); 0.8 µl of 10 µM primer; 0.1 µl Taq DNA polymerase (5 U/µl); 1.2 µl template DNA (approx. 25 ng/µl). The reactions were run through four initial "touch down" cycles (94° C for 1 min; 35° C for 1 min; 0.3 slope to 72° C for 2 min), and then 32 amplification cycles (94° C for 10 s; 35° C for 30 s; 72° C for 30 s). The finished reactions were held at 4° C until they were visualized. For visualization, the amplified products were run out on a 1.2% agarose gel (80–120 V), stained with ethidium bromide, then visualized and photographed under UV light.

Paternity analysis.—RAPDs are dominant markers, and band presence/absence is particularly sensitive to reaction conditions because of the short length of the primers. Therefore, repeatability of RAPD markers has been problematic, making them not as robust in parentage analyses as some other molecular techniques (e.g., microsatellites or multilocus minisatellite DNA fingerprinting; for review see Parker et al. 1998). In this experiment, however, RAPDs were useful to assess paternity of broods because the pool of potential fathers is limited and known, and because repeatability was confirmed. A unique bands analysis was used to assign the father of each brood member. On the gels, the mother and two potential fathers were run as triads twice, flanking the offspring lanes. Bands that were observed in the lanes of one of the males, but not in the lanes of the other male or mother, were scored for their presence in the offspring lanes. Multiple primers were screened for the families until a total of at least two diagnostic bands were found for each juvenile. Such an analysis is simple and robust since no inference is made from band absence, and the

repeatability of each diagnostic band is confirmed by amplifying the triads of adults twice, and running them on the flanking lanes on both sides of the gels.

RESULTS

Mating behavior.—When the males were placed in the containers near the females, they would typically remain motionless for up to 1 min. They would then begin to move around in the web while rapidly drumming their first pair of legs on the silk. The movement of the males appeared undirected until the females moved within the web, at which point the males would begin to move toward the females while still drumming. As the males approached, the females would typically bounce in the web apparently signaling sexual receptivity because the males would move more quickly toward them afterwards. The males continued drumming even as they made contact with the females. The males would orient themselves to face the same direction as the female, with their ventral surfaces adjacent, but with no consistent absolute orientation. As the males moved into position, the amplitude of their drumming eased to a stop, which was taken to be the onset of copulation. After copulation the spiders separated with a conspicuous jerk, followed by the males moving a short distance from the females (1–2 cm). If only one copulation had taken place, the males would resume drumming and repeat the courtship, but would typically move in more quickly and insert on the other side. The females in this experiment, in all cases, appeared receptive to both males. Also, no occurrences or apparent attempts of sexual cannibalism were observed.

As measured by the number of copulation onsets and breaks, first males had fewer copulations (mean 2.2, range 2–4) than second males (mean 3.7, range 2–12; Mann-Whitney $U = 489$, $P < 0.001$, Fig. 1). Only three of the 25 first males had more than two copulations, and in those cases there were one or two short copulations followed by two long ones. The total time spent in copula was longer for first males (mean 44.3 min, range 34.7–52.4) than for second males (mean 15.9 min, range 1.5–42.1; $t = 11.3$, $P < 0.001$, Fig. 1). In six cases the second males had more than three copulations, but their total time of copulation (mean = 11.0 min) was significantly shorter than the second males that had three or fewer copulations (mean = 19.6; $t = 1.9$, $P = 0.04$). Considering individual females, their first mate's total time of copulation was not related to their second mate's total time (Fig. 2). The duration of the first male's first copulation was a strong predictor of the duration of his second copulation (in cases where there were more than two copulations, the initial apparent "false starts" [copulations lasting less than one minute] were excluded: Fig. 3).

Paternity analysis.—Of the 25 females in the mating experiment, 22 produced egg cases, of which 17 had juveniles emerge (which was considerably lower than the mean of 36 juveniles observed in nature; Brach 1977). The average number of juveniles per family was 11.6 (range 4–21). Two of the families were unusable because one of the males (in each family) could not be amplified by PCR. Of the fifteen remaining families, all 168 of the juveniles were assigned to the first male. While the assignments were based on the presence of at least two of the first male's unique bands, the lack of the second male's unique bands in juvenile lanes further confirmed the assignments.

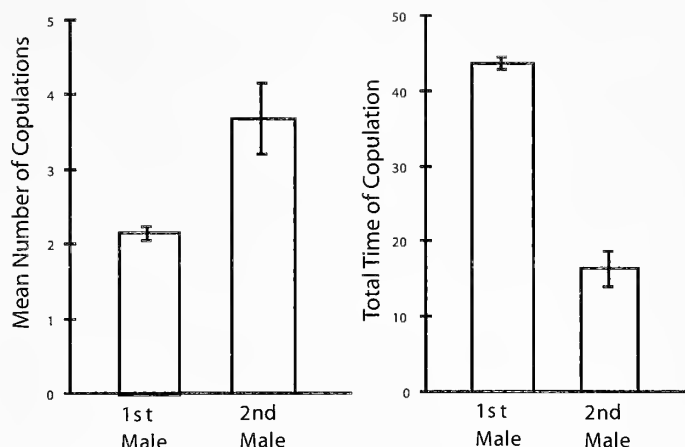


Figure 1.—Comparison of the mean number of copulations and total duration of copulation between first and second males in *Anelosimus studiosus*. Reported are means with standard error bars.

DISCUSSION

Using a direct DNA-based analysis of parentage, we found complete first male sperm precedence in *A. studiosus*. We also found significant differences in the mating behavior of first and second males. The patterns of sperm precedence, the increased frequency of starting and stopping copulation with less actual time spent in copula of second males, suggests that the second males could not successfully copulate.

There is evidence from other spider species that second males can be prevented from successfully copulating. Copulation "plugs" made by a hardening of seminal fluids in the female reproductive tract or by the tip of the male's intromittent organ breaking off, have been reported for several spider species *Phidippus johnsoni* Peckham & Peckham 1983 (Jackson 1980), *Agelena limbata* Thorell 1897 (Matsumoto 1993; Yoward & Oxford 1996; Schneider et al. 2005). However, the efficacy of these plugs in preventing subsequent

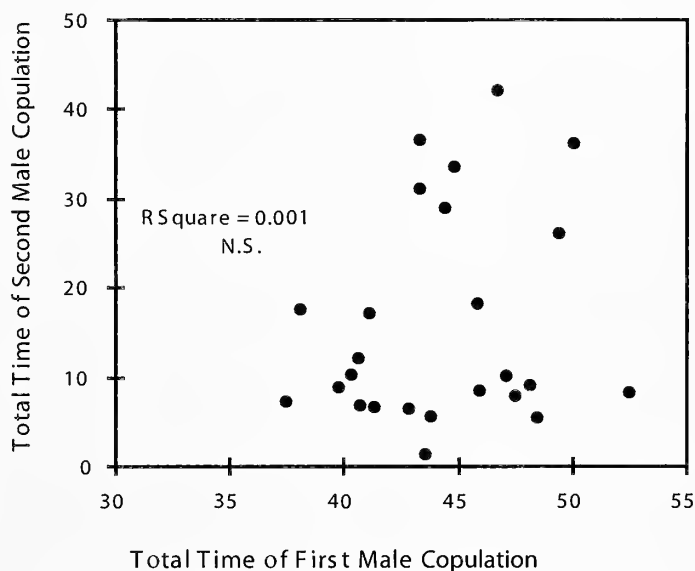


Figure 2.—Plot of a female's total time of copulation with the first male versus her total time of copulation with the second male in *Anelosimus studiosus*.

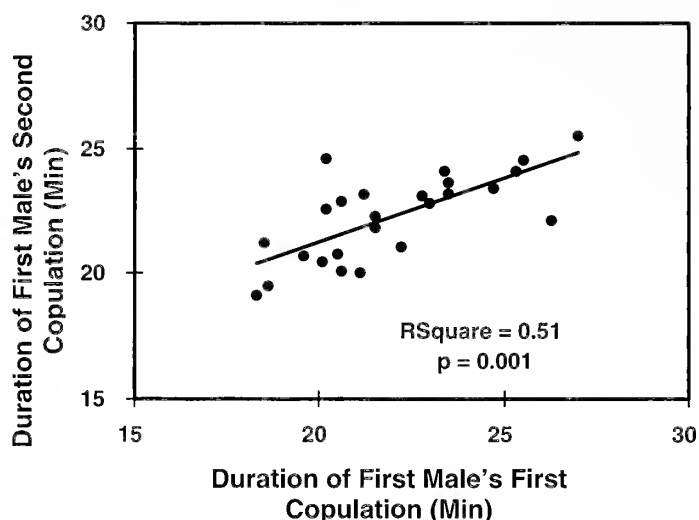


Figure 3.—Plot of the duration of the first male's first copulation versus the total time of his second copulation in *Anelosimus studiosus*.

fertilizations is mixed among taxa, and they may instead function to increase the sperm retention and survival (reviewed in Huber 2005). In another theridiid spider, fertilization patterns are affected by where the broken organ tip rests in the female reproductive tract (Snow et al. 2006). Across spider taxa, male genital mutilation appears to be an indicator of strong selection on paternity protection, being correlated with the evolution of male sacrifice behavior and size dimorphism (Miller 2007). We did not determine in this study whether or not the second male was in any way prevented from copulation. The fact that four of the second males' copulatory behavior was similar to the first males' (having two intromissions totaling > 30 min), suggests that copulatory plugs are not ubiquitous, or at least not completely effective. However, we have observed a second male repeatedly moving in and breaking from a female, apparently struggling to insert his palps.

Interestingly, first male total copulation time was only 16% that observed in a congener (Klein et al. 2005). The fact that second males spent less total time in copulation contradicts previous findings in an araneid spider (*Micrathena gracilis* Walckenaer 1805) in which second males copulated over twice as long as the first male (Bukowski & Christenson 1997b), but similar to patterns found in a tetragnathid spider (*Tetragnatha versicolor* Walckenaer 1842; Danielson-Francois & Bukowski 2004). In the latter case sperm release was equal between first and second males. A similar experiment in which males were introduced to females that had only been mated on one side of their tract suggested that males are responding specifically to the reproductive status of the female's reproductive tract, rather than the female's behavior or overall condition (Bukowski et al. 2001). Second males also copulated for shorter periods in a cellar spider, *Pholcus phalangioides* Fuesslin 1775 (Schafer & Uhl 2002). In this case, however, the second males had a higher proportion of reproductive success, apparently as a result of their ability to remove the first male's sperm.

Since second males generally attempted copulation, the differences in their mating behavior seems most likely because they are prevented from normal copulation. The possibility

remains however, that they could be altering their behavior in response to the previously mated condition of the female. There are examples of non-virgin spiders being less attractive to males. The presence of sex pheromones has been documented across a wide range of spider species and, in some cases, these pheromones are volatile (Shultz & Toft 1993; Miyashita & Hayashi 1996; Rovner 1996; Costa et al. 1997; Searcy et al. 1999), and in other cases are contact based (Trabalon et al. 1997, 1998). In one linyphiid spider (*Nereine litigiosa* Keys 1886) pheromones are incorporated in the female's web, and males destroy the web prior to mating, reducing the probability that a second male will find her (Watson 1986). Whether pheromones exist in this species is not known, but pheromone-like compounds have been extracted from the cuticle of its congener *A. eximius* (Bagnères et al. 1997). It is possible that, even though the female remains sexually receptive after mating, her production of pheromones decreases, thus making her less attractive to second males. The speed with which the first and second males begin drumming and searching for the female might give insight into pheromone levels, but such a measure would be confounded by the introduction of the males, which was not standardized in terms of their distance from the female.

This study found complete first male sperm precedence, accentuating the question why an *A. studiosus* female should mate multiply at all. There are many potential costs to mating such as loss of foraging opportunities, increased predation risk, and disease transmission (reviewed in Lewis 1987). Male spiders provide no parental care, and it is unlikely that any substances that males transfer along with sperm provide direct benefits to the females as has been observed in some insects (Gwynne 1984; Boggs 1990). With linyphiid spiders the male cohabitates in the female's web, eating prey, until he has mated with her; females apparently mate with these males to induce them to leave (Watson 1993). However, there is evidence from the same species that multiple mating has indirect benefits in terms of the size and growth rate of juveniles (Watson 1998). In the pisaurid species *Pisaura mirabilis* (Clerk 1757), in which females mate with multiple males, males present nuptial prey items (Drengsgaard & Toft 1999). Mating multiply allows the possibility of cryptic female choice in which she chooses the sperm of the male she prefers (Eberhard 1996). Again, given complete first male precedence, this seems unlikely to be occurring with this species. Perhaps the simplest benefit to a female from multiple mating would be to ensure that all her eggs get fertilized. It may also be that there is no selective benefit to mating with multiple males, and that *A. studiosus* females simply remain receptive from maturity until their abdomens are distended with eggs regardless of the number of times they have mated.

Previous work on this species has demonstrated that by delaying dispersal and remaining part of their natal colony, juveniles enhance their survival and development (Jones & Parker 2002). This can be extrapolated to suggest that juveniles' direct fitness benefits from delayed dispersal. This study finds complete first male sperm precedence within the broods of doubly-mated *A. studiosus* females. This suggests that if an individual juvenile's presence in the colony contributes to the survivorship of its brood-mates, its indirect fitness (sensu Hamilton 1964) would be maximized because

they are all full-sibs. In this species it is now documented that there are colonies that contain multiple adult females in North America (Furey 1998), the incidence of which increases with latitude (Jones et al. 2007). If these colonies develop by non-dispersal of juveniles, fertilization patterns could have profound effects on the genetic structure of these large colonies.

Finding complete first-male sperm precedence may be surprising, but these results should be taken with some caution given the highly controlled conditions. Factors such as the number and timing of matings, which may influence precedence (Eberhard 1996), were held constant. Currently studies are underway exploring relatedness within and among natural colonies using microsatellite loci.

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Frequency and consequences of damage to male copulatory organs in a widow spider

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Abstract. Copulatory organ breakage, in which a portion of the male's genitalia breaks off and remains in or attached to the female's genitalia may represent a male strategy of high investment in a single mating. Such a strategy is expected when mating opportunities for males are limited and competition for females is high. We studied costs and benefits for males as a consequence of male organ breakage in the white widow spider (*Latrodectus pallidus* O. Pickard-Cambridge 1872). In order to estimate the frequency and consequences of such damage we provided each male with four virgin females simultaneously in an outdoors enclosure. We recorded male mating success and loss of the tip of the embolus (the male intromittent organ) inside the female's genitalia for each male. In order to test the effect of the broken tip as a mating plug, we collected females from natural populations and observed the location of embolus tips inside their genitalia. We found that damage to the male organ was frequent but did not necessarily result in male sterility. From the field data, we found that the likelihood of a second embolus tip entering the spermatheca is significantly lower than that of the first tip, suggesting the possibility that the tip functions as a partial mating plug.

Keywords: Male mating strategy, embolus tip, *Latrodectus pallidus*

The reproductive success of a male is usually a function of the number of females he inseminates, especially when males produce numerous gametes and when little time and energy is spent on care of offspring. Under these circumstances each male is expected to mate with many females (Darwin 1871; Bateman 1948; Trivers 1972; Andersson 1994). Nevertheless, in some cases males invest highly in a single female. This investment may increase the male's reproductive success in the current mating but dramatically reduce the number of matings that he can potentially achieve. Such a strategy can be promoted by evolutionary processes if the probability of encountering and mating with an additional receptive female is sufficiently low (Parker 1979; Buskirk et al. 1984; Elgar 1992; Simmons et al. 1992; Parker 1998; Andrade 2003) and if males strongly compete for females (Thornhill 1980; Fromhage et al. 2005).

Copulatory organ breakage, in which a portion of the male's genitalia breaks off during copulation is relatively common in spiders (Wiehle 1967; Breene & Sweet 1985; Foelix 1996; Schneider et al. 2001; Miller 2007). Broken organs inside the female's genitalia may function as a mating plug to prevent fertilization by later arriving males, but it may also reduce the probability of the male fertilizing additional females (Foelix 1996). Thus, this trait may represent a male strategy of high investment in a single mating. To date, few studies have quantified the costs and benefits of male organ breakage. In the spider *Nephila fimestrata* Thorell 1859, for example, males often damage both of their paired mating organs while copulating with a single virgin female (Fromhage & Schneider 2005). The occurrence of a male organ part inside the female's genitalia was shown to reduce the number of copulatory insertions by a second male (Fromhage & Schneider 2006). Similarly, in *Argiope bruennichi* Scopoli 1772, males can use

each copulatory organ once, and insertions into a previously used insemination duct were significantly shorter when the previous male had left parts of his genitalia inside the insemination duct (Nessler et al. 2007).

In widow spiders (*Latrodectus*), the tip of one or both of the male's intromittent organs (emboli) often breaks-off during copulation to be left inside the female's genitalia (Levi 1959; Bhatnagar & Rempel 1962; Wiehle 1967; Kaston 1970; Berendonck & Greven 2002; Segoli et al. 2006). Males without embolus tips were assumed to be functionally sterile (Bhatnagar & Rempel 1962; Foelix 1996), but there is evidence that this is not always the case, as shown in *L. mactans* Fabricius 1775 (Breene & Sweet 1985) and *L. hasselti* Thorell 1870 (Snow et al. 2006). It was suggested that a tip inside the female's spermatheca functions as a mating plug (Foelix 1996; Berendonck & Greven 2002); however, this was demonstrated only in *L. hasselti*. In this species first male sperm precedence was found when two males inseminated a single genital pore (Snow & Andrade 2005) and when the first tip was deposited in the entrance of the spermatheca (Snow et al. 2006). In several other *Latrodectus* species, however, more than one tip can be found inside the female's spermathecae (Uhl 2002), suggesting that the embolus tip is not totally effective as a mating plug.

In this study we investigated two aspects of the adaptive value and costs of damage to the male organ in the white widow spider, *Latrodectus pallidus* O. Pickard-Cambridge 1872: 1) future inseminating opportunities for males who have broken emboli (male sterility hypothesis) and 2) the risk of sperm competition (mating plug hypothesis). Males of this species suffer high extrinsic mortality and normally do not encounter more than one female in natural conditions, while females are often polyandrous (Segoli et al. 2006). Thus, males

that encounter a virgin female would benefit from blocking the spermatheca of their mate and thereby reducing or preventing access to future rivals. There is evidence that *L. pallidus* males invest highly in each mating: they cohabit in females' webs longer than required for mating (Segoli et al. 2006), engage in an energetically demanding courtship display (M.S. personal observations), and are sometimes cannibalized by the female (Segoli et al. 2006). Thus, breakage of the male organ may be an integral part of the male mating strategy in this species even at the cost of a limited fertilization success in the future.

In order to estimate the frequency and consequences of male organ breakage we asked the following questions: 1) How frequently do embolus tips break? 2) Does the loss of embolus tips prevent the male from remating? and 3) does the presence of a tip inside the female's spermatheca reduce the probability of another tip entering the spermatheca? In order to answer the first two questions we conducted an experiment in which we provided 21 males each with four virgin females simultaneously in outdoor enclosures. Thus, each male had the opportunity to possibly mate with four females. For each male, we recorded fertilization success and the loss of embolus tips by recording the successful production of viable egg sacs in females and by recording the presence of the embolus tips in the genitalia of the females. In order to answer the third question, we collected females from natural populations and recorded the location of male tips inside their genitalia.

METHODS

The white widow spider (*L. pallidus*) is common in the Negev desert of Israel (Levy 1998). We collected males and females from the Sede Teman area (31°17'N, 34°43'E) and Sayeret Shaked Park (31°16'N, 34°38'E) (northern Negev, Israel) in April 2003. Voucher specimens were deposited in the National Collection of Arachnids, Hebrew University of Jerusalem. Spiders were collected as juveniles or sub-adults and reared to maturity under lab conditions on the Sede Boqer Campus of Ben-Gurion University. Males were kept in plastic cups (200 cc) and fed weekly with *Drosophila*. Females were kept in terraria (10 × 20 × 15 cm) containing small dry shrubs, on which they constructed their webs. Females were fed weekly with flour beetles (larvae of *Tenebrio molitor*), crickets (*Acheta domestica*), grasshoppers (*Schistocerca* sp.) and houseflies (*Musca domestica*).

Enclosure experiment.—We placed four adult virgin females with their webs in a square outdoor arena (135 cm length × 135 cm width × 50 cm height), one in each corner. Each arena was constructed from a wooden base and frame with plastic sheets as walls and a removable mesh cover. Females were not fed during the trial. Once the females repaired their webs (~1 day), we placed one adult naïve male in the center of each arena ($n = 21$ replicates). The location and activity of the male (no movement, courting, in mating position) were recorded three times a day until it died. The number of daily observations was determined from preliminary observations, which indicated that males stay at least one day with each female. Females were measured and weighed at the end of each trial. They were kept until they produced seven egg sacs or until two months passed without laying eggs. Females that produced fertile egg sacs were assumed to have mated. This assumption is valid because mated females kept with adequate

food rarely fail to produce fertile egg sacs (M.S. personal observations). The reproductive success of females was measured by the total number of eggs and by the number of fertile eggs (eggs that hatched) from the first five egg sacs. We used data from the first five egg sacs since most females lay 1–3 egg sacs in the field and five egg sacs was the maximum observed in nature (M.S. personal observations). Post mortem we checked females' spermathecae for the presence of embolus tips. Females have paired copulatory ducts, each leading to a spermatheca, and males have paired intromittent organs (emboli). During mating, the male inserts one embolus at a time into one of the female's genital openings. Thus, a male may leave none, one, or both tips (one in each side) in the genitalia of a female. We obtained complete data on male embolus tips in the genital tracts of all four females from 15 trials. Spermathecae were examined by placing them in a 5% KOH solution; after a week the tissue became transparent and the embolus tips were visible under a dissecting microscope (Berendonck & Greven 2002). For each trial we determined the order and number of females the male visited, which of the females he inseminated, the reproductive success of each female and finally, which females possessed embolus tips inside the spermathecae.

Females collected from the field.—We collected 216 adult females from their webs at three locations in Israel: Goral Hills, near Lehavim (31°22'N, 34°49'E, $n = 192$), Kfar Edomim (31°49'N, 35°19'E, $n = 13$), and Sayeret Shaked (31°16'N, 34°38'E, $n = 11$) from March 1998 till September 1999. Egg sacs, if present, were left unharmed in the web. We dissected the females, removed their spermathecae and copulatory ducts, placed them in a 5% KOH solution and examined them for the presence of embolus tips as above. Since the number of tips in the right and left genitalia were correlated (Spearman rank correlation, $n = 216$, $R_s = 0.632$, $P < 0.01$), we considered only the right spermatheca and copulatory duct of each female, thereby avoiding pseudoreplication.

We compared cases in which one male tip was found in the female genitalia (genital duct + spermatheca) to cases in which two tips were found. We estimated the probability of a first embolus tip to enter the spermatheca as the percentage of females with an embolus tip located inside the spermatheca out of the total number of females with one embolus tip found in their right genitalia. We compared this with the probability of a second tip entering the spermatheca: the percentage of females with two tips inside the spermatheca, out of the total number of females with two tips in their right genitalia. We expected that if the first tip prevents the second tip from entering the spermatheca, the probability of finding a second tip inside the spermatheca would be lower than for the first tip.

RESULTS

Enclosure experiment.—After placement in the arena with the four females, males started courting one of the females. Courtship included the following behaviors: adding silk to the female's threads, vibrating the web and cutting sections from the web. Mating was difficult to observe since it took place inside the female's retreat. On the following days males were observed courting or standing motionless on the web, either inside or outside the retreat. The median time from the

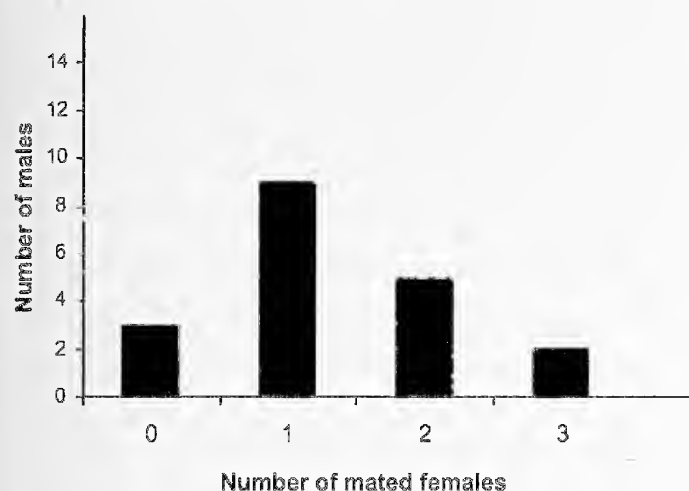


Figure 1.—Number of males that mated with 0–3 females ($n = 19$ trials). Each male was provided with four virgin females simultaneously in an outside enclosure.

introduction of the male into the arena with females until the death of the male was 5 days (range 1–23 days, $n = 21$). One male escaped from his arena and entered another arena. He was returned to his arena after visiting one female in the adjacent arena. We excluded the two males from these two arenas from analyses of the number of mated females.

Three males out of 19 did not inseminate any female, most of the males inseminated one or two females and two males inseminated three females (Fig. 1). The proportion of inseminated females was higher among females that were visited first (77%) than among females visited later (41%) (Fisher's exact test, $n = 22$ for first females and $n = 29$ for females visited later, $P = 0.02$).

Three mated females died during the experiment and the remaining mated females produced seven egg sacs before the end of the experiment. The mean number of eggs per egg sac was 130 ± 30 (\pm SD, $n = 30$ females; averages of eggs per sac for each female were averaged over all females) and the number of hatched eggs was 103 ± 40 . The total number of eggs that were produced by mated females in the first five sacs was not influenced by the number of embolus tips inside their spermathecae nor by mass, size, or age of females (GLM stepwise backward model, $n = 25$, $P > 0.1$ for all). The results were still not significant when considering hatched eggs only. Thus, there were no differences among the females in their reproductive success.

Six out of 21 males (29%) were cannibalized by females. Cannibalism was observed directly or could be inferred from the transparent body of the dead male found on the female's web. In five out of six cases the cannibalistic female did not produce egg sacs, indicating that cannibalism occurred before copulation, or that the female did not use the male's sperm for fertilization.

Data on the presence of male embolus tips in the genitalia of females and fertilization success are presented in Table 1. Three males did not lose any embolus tip with the first female they visited; nevertheless, one of these fertilized the female. Four males lost one embolus tip in the first mating. Two of these fertilized the first female only and the other two fertilized one and two additional females. Eight males lost both embolus

Table 1.—Embolus tips inside spermathecae and fertilization of 1st, 2nd, and 3rd females visited by 15 males in the arena experiment. Numbers in columns represent the number of tips found in the female spermathecae. Shaded cells indicate that the female produced fertile egg sacs.

# males	First	Second	Third
2	0	0	0
1	0	0	0
2	1	0	0
4	2	0	0
3	2	0	0
1	2	0	0
1	1	1	0
1	1	1	0

tips in the first mating. Four of these fertilized the first female only, three fertilized an additional female, and one fertilized two additional females.

Females collected from the field.—Forty-eight out of 216 females contained no embolus tip inside their right genitalia. In 86 cases out of the 95 females that contained one tip in their genitalia, the tip was placed inside the spermatheca, and in nine cases the tip was located in the genital duct. Thus, we estimated the probability for the first tip in the female's genitalia to enter the spermatheca as 0.9. We found 58 females with two embolus tips inside their right genitalia. Out of these, in three cases both tips were located in the genital duct, in 28 the two tips were placed inside the spermatheca, and in 27 one tip was placed inside the spermatheca and the second was in the genital duct. Thus, we estimated the probability of a second tip to enter the spermatheca as 0.5. The likelihood of a first tip to enter the spermatheca was significantly greater than the likelihood of a second tip to enter the spermatheca (Fig. 2, Fisher's exact test, $P < 0.0001$). Additionally, fourteen females contained three tips in their right genitalia. Of these, one female had no tips inside the right spermatheca, 8 had one tip, two had two tips and three had three tips. Finally, one female contained five embolus tips, four of which were found inside the spermatheca.

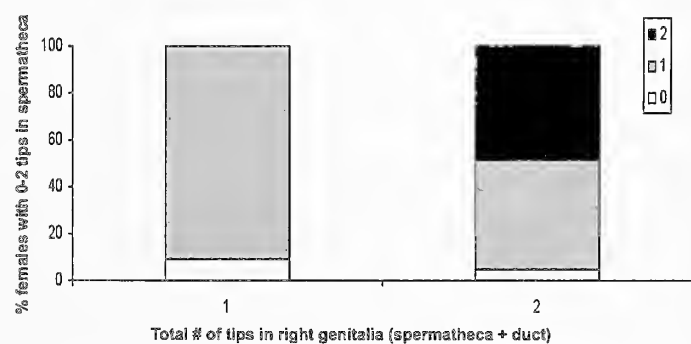


Figure 2.—Embolus tips found in the spermatheca alone and in the entire genitalia: percentage of females with no embolus tips (white section), one embolus tip (gray section) or two embolus tips (black section) inside their right spermatheca, out of field-collected females with either one ($n = 95$) or two tips ($n = 58$) in their right genitalia (spermatheca + genital duct).

DISCUSSION

In this study we estimated the frequency and consequences of damage to the male copulatory organ in the white widow spider *L. pallidus*. We found that damage to the male organ was frequent but did not necessarily result in male sterility. We showed that the occurrence of a male's embolus tip inside the female's spermatheca functions as a partial mating plug: it probably obstructs but does not always prevent the entrance of an additional tip into the spermatheca.

In contrast to our study, male sterility following damage to the male copulatory organ has been demonstrated in several spider species. For example, in *Argiope keyserlingi* Karsch 1878, experimental removal of one copulatory organ prevented males from copulating with more than one female, suggesting that males can use each of their paired organs only once (Herberstein et al. 2005). In *Nephila funestrata*, 95% of the males mating with a virgin female had a damaged organ that probably prevented them from remating (Fromhage & Schneider 2005). In widow spiders the loss of an embolus tip inside the female genital tract was previously assumed to result in functional sterility of the male (Bhatnagar & Rempel 1962). Breene & Sweet (1985), however, found that some males of a congener (*L. mactans*) were able to successfully inseminate three females suggesting that males either do not always lose their tips or that they can inseminate in spite of embolus breakage. In *L. hasselti*, males are normally sterile after mating (Andrade & Banta 2002), but when tips were cut experimentally males were able to inseminate additional females (Snow et al. 2006). Thus, the loss of embolus tips alone cannot be responsible for the post-mating sterility in *L. hasselti*. In our study we found that at least one male mated and inseminated a female without losing any embolus tip and five males inseminated one or two females after losing both tips in previous matings. Thus, we suggest that the loss of embolus tips in *L. pallidus* is common, but does not prevent the male from fertilizing additional females.

Although damage to the copulatory organ in *L. pallidus* was not an absolute constraint on the male's reproductive success, only a few males (2 out of 19) inseminated more than two females. This suggests that insemination with a broken embolus is mechanically difficult and is less likely to be successful than insemination with an intact embolus. Additionally, in the absence of tips, males may have difficulties filling their emboli with sperm (sperm induction) and therefore low fertilization success may result from sperm depletion rather than an inability to transfer sperm (Snow et al. 2006). However, it is not yet known whether white widow males refill their emboli between mating attempts. Finally, insemination with a broken embolus may be especially difficult when mating with an already mated female with a plugged spermatheca. If so, embolus breakage may still carry a cost for males in mating systems where sperm competition exists.

Although males were not competing for females in this experiment, there is evidence that embolus breakage may give the males an advantage in sperm competition. Most of the males that lost both tips (8 out of 10) left them in each of the two spermathecae of the first female that they mated, indicating that they had mated with her twice. However, there was no difference in the reproductive success of females with one or two tips in their spermathecae. A similar result was

obtained in a study of *L. hasselti* where repeated mating did not increase the probability of successful fertilization nor the number of offspring produced in successful matings (Andrade & Banta 2002). We suggest that males leave both tips in order to protect both of the female's spermathecae from future insemination by rival males.

The analysis of spermathecae from females collected in the field further supports the view that the broken embolus functions as a partial mating plug. The probability of a first embolus tip entering the spermathecae was significantly higher (90%) than that of the second tip (50%). It is also possible that a second tip replaced the first, but this is unlikely considering the narrow entrance to the spermatheca (Barendonck & Greven 2002). However, the results also suggest that the tip is not totally effective as a plug: in half of cases a second tip **did** enter the spermatheca, and in four cases more than two tips entered the spermatheca. In contrast, in a study of *L. hasselti* it was shown that in ~90% of the cases where two males inseminated the same genital pore, the second tip did not enter the spermatheca resulting in a first male sperm priority (Snow et al. 2006). Although it is difficult to compare the results of this controlled experiment with our field data, it implies that the plug in *L. hasselti* is more efficient than in *L. pallidus*. From an evolutionary point of view, the differences in the efficiency of the plug between species may reflect an arm-race between males and females over control of paternity. In this light it would be interesting to compare the efficiency of the plug in different *Latrodectus* species in relation to mating opportunities, effective sex ratio, and sexual cannibalism.

In contrast to embolus tip breakage, sexual cannibalism does not seem to be an integral part of the male mating strategy in *L. pallidus*. In *L. hasselti*, males initiate cannibalism by placing their abdomen in front of the female's mouthparts during copulation: cannibalized males copulate longer and cannibalistic females are less likely to remate (Andrade 1996). Similar sacrificial behavior was also observed in *L. geometricus* C.L. Koch 1841 (Segoli et al. 2008). In *L. pallidus*, however, most of the cannibalized males (5 out of 6) did not fertilize the cannibalistic female and thus could not benefit from cannibalism. This illustrates the distinction between male sacrifice behavior as an adaptive strategy and cannibalism as an unavoidable consequence of mating with a dangerous partner.

In conclusion, damage to male copulatory organs is consistent with a male strategy of high investment in a single female. Embolus damage does not necessarily result in male sterility and may provide some paternity advantage over subsequent males. This benefit will be expressed only when females mate multiply and when mating opportunities are limited for males, as is the case in the mating system of white widow spiders (Segoli et al. 2006).

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Molting interferes with web decorating behavior in *Argiope keyserlingi* (Araneae, Araneidae)

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Abstract. Various orb weaving spiders decorate their webs with extra silk structures. In the araneid genus *Argiope*, these web decorations consist of flimsy aciniform silk threads arranged in zig zag shaped bands. The adaptive value of these structures is still unclear and controversy over a suite of possible functional explanations persists: the high variation of web decoration adds further uncertainty. Web decorations can differ in shape, size, and frequency across species and even within species. Physiological processes may influence individual variation in web decorating behavior. Molting events are major physiological transitions combined with fundamental alterations of the metabolic state of the spiders. For gaining new insights into possible proximate mechanisms driving web decorating behavior, we observed subadult *Argiope keyserlingi* Karsch 1878 females in the laboratory and registered the individual variation of web decorations associated with the maturity molt under laboratory conditions.

We found substantial individual variation of web decorations of *A. keyserlingi*. The most striking result was that subadult spiders built dramatically oversized decorations prior to the last molt. Since aciniform silk is used for both constructing web decorations and immobilizing prey we suggest that these extensive decorations might provide a store for the swift replenishment of aciniform silk after the molt. High silk recycling rates make temporary outsourcing less costly and facilitate a rapid resumption of prey capture following lost foraging opportunities during the molting phase. Thus, we argue that the solution of the riddle of web decorations might reside in the physiology of molting spiders.

Keywords: Orb-web spiders, web decorations, maturity molt, gland regulation

Web decorating is a characteristic behavior of various orb weaving spiders (Robinson & Robinson 1973; Edmunds 1986; Bruce 2006), yet the possible functional explanations remain controversial despite extensive investigations (Herberstein et al. 2000; Eberhard 2003; Bruce 2006). “Web decorations” (first mentioned as such by McCook 1889, but also called “stabilimenta” by Simon 1895 and many modern authors) in the araneid genus *Argiope* consist of numerous flimsy aciniform silk threads (Peters 1993), mostly arranged in zig zag shaped bands (Bruce 2006). Although web decorations of *Argiope* are considered as prey attractants by some (Craig & Bernard 1990; Tso 1996; Bruce et al. 2001; Li 2005; Cheng & Tso 2007), this view is not unanimous and alternative functional explanations include anti-predator devices (Ewer 1972; Schoener & Spiller 1992; Blackledge & Wenzel 2001); advertisement for web protection (Eisner & Nowicki 1983; Kerr 1993; Blackledge & Wenzel 1999); thermoregulation (Humphreys 1992); mechanical support [Robinson & Robinson 1970; see also Watanabe 2000 for *Octonoba sybotides* (Bösenberg & Strand, 1906), Uloboridae]; and acting as a molting platform (Robinson & Robinson 1973, 1978). In the rapidly growing literature on this topic, tests for non-visual functions are clearly underrepresented (Bruce 2006). In particular the potential relationship between physiological processes and web decorating behavior has been addressed in only a very few studies (e.g., Peters 1993; Tso 2004; Walter et al. 2008a).

Typically, decorating behavior in species of *Argiope* is highly variable (Bruce & Herberstein 2005) and web decorations can differ in shape (number and arrangement of zig zag bands), size and frequency (Lubin 1975; Edmunds 1986; Nentwig & Heimer 1987; Schoener & Spiller 1992). One problem for determining the adaptive value of web decorations stems from this high variation (Robinson & Robinson

1974), which occurs across species and within species at both the population and individual level (Herberstein et al. 2000; Starks 2002; Bruce & Herberstein 2005; Rao et al. 2007). Most studies explore the adaptive significance of these structures (e.g., Blackledge 1998; Craig et al. 2001), although phylogenetic analyses of web decoration patterns suggests that interspecific variance shows weak homologies at best and yields phylogenetically feeble signals (Herberstein et al. 2000; see also Scharff & Coddington 1997). We agree with Eberhard (2003) that an accumulation of single “experiments *per se* ... are no guarantee of reliable conclusions.” Thus, understanding the intra-individual variance of web decorations in detail is necessary before embarking on the interpretation of web decorating behavior in general.

The production of web decoration is governed by an enhanced activity of the silk glands and hence physiological processes are expected to impact web decorating behavior (Tso 2004; Walter et al. 2008a). The major physiological transitions in the life history of spiders are the repeated molting events. Molting requires a drastic change of anabolic and metabolic biochemical pathways requiring fundamental alterations of the physiological state of the animal. Apart from hormonal changes (Bonaric 1987; Foelix 1996; Craig 2003), molts are particularly vulnerable events in the life of spiders, in terms of both increased physiological stress (Pulz 1987; Vollrath 1987a) and increased risk of predation (Tolbert 1975; Tanaka 1984; Vollrath 1987b; Baba & Miyashita 2006). It would, therefore, be surprising if web decoration behavior was not affected by molting. Indeed several studies suggest that molting might have profound effects on the web decorating activity of *Argiope* (Robinson & Robinson 1970, 1973; Edmunds 1986; Nentwig & Heimer 1987). Yet if we observe consistent changes in the patterns of decoration behavior associated with the molting process, this might

provide insights into the proximate mechanisms driving web decoration and their potential adaptive value.

METHODS

Study species and experimental design.—We chose the St. Andrew's cross spider, *Argiope keyserlingi* Karsch 1878, to study the variation in web decoration under highly controlled laboratory conditions. This orb web spider is distributed along the east coast of Australia (northern Queensland to Victoria in the south), building their webs between branches and leaves of bushes, e.g., in parks and gardens. *Argiope keyserlingi* is a well studied species in terms of its natural history (Rao et al. 2007), its sexual cannibalism (Elgar et al. 2000; Herberstein et al. 2005) and its web decorating behavior (Herberstein 2000; Bruce et al. 2001, 2005; Herberstein & Fleisch 2003). St. Andrew's cross spiders typically build cruciate web decorations consisting of up to four zig zag bands forming a large "X" in the orb web (Rao et al. 2007). This allows an unambiguous interpretation of deviations from the "complete cross."

We collected 55 subadult female spiders in Ku-ring-gai Bicentennial Park (West Pymble/Sydney, Australia) and transferred them individually to Perspex frames (58 cm × 58 cm × 15 cm) in the laboratory, where they were kept under natural light conditions. Every other day, each spider was fed with one blowfly (*Lucilia* spp.). At this life stage the spiders are still of a similar size as the blowflies; thus, it has turned out in preliminary observations that this feeding regime is sufficient to keep spiders "well-fed." At this same time, each web was moistened with five shots from a water spray. Given that spiders typically build a new web each day, we recorded daily the number of decoration bands (shape) and decoration size to assess the variation of web decorating behavior within a total observation period of 30 days. We estimated the size of the web decoration by computing a trapezium area similar to Tso (1999): $(a+c)/2 \times h$ (a and c = upper and lower width of zig zag bands, h = height of zig zag bands, see Fig. 1). Additionally, we quantified the size of all newly built webs following Herberstein & Tso (2000): $(d_v/2) \times (d_h/2) \times \pi$ (d_v = vertical and d_h = horizontal diameter of the capture area, see Fig. 1) and measured the spider body size (length from clypeus to the end of the opisthosoma). Voucher specimens were deposited in the Entomological Collection of the Martin-Luther-University Halle-Wittenberg (Zoological Institute), Germany (identification number 2569).

Statistical analyses.—We used STATISTICA® (version 6.0) for all statistical analyses including the paired t -test to evaluate differences in the sizes of decorated and undecorated webs. Chi square-tests and t -tests were used to detect differences in the proportion of decorated web parts and constructed decoration patterns. Web and web decoration sizes prior, during, and after molting events were analyzed with an ANOVA. Pearson-correlations were computed between web size and decoration size.

RESULTS

Web decorating frequency.—All females could be observed over the whole 30 day period. Forty-six of the 55 subadult *A. keyserlingi* molted to maturity within this time. The spiders constructed new webs every second day (mean 2.29 ± 0.07 SE day). Typically, the new web decorations were built together with new webs, and therefore the decorating activity mostly

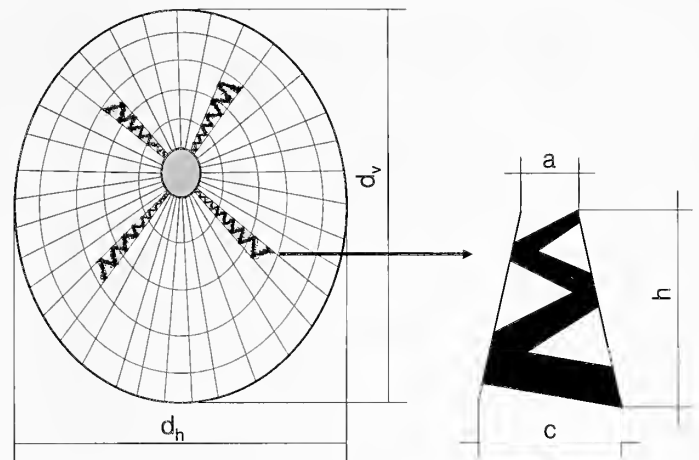


Figure 1.—Web and decoration measurements from the webs of *A. keyserlingi*: Left: determination of the size of capture areas (including hub region), d_h = horizontal diameter, d_v = vertical diameter; Right: determination of decoration band sizes, a = upper width of the band, c = lower width of the band, h = length of the band (lettering after trapezium formula).

followed an equal rhythm (a mean value of every 2.37 ± 0.37 SE day). The few exceptions were all in the context of molting events (see below). However, 233 (37.5%) of all newly built webs ($n = 622$) did not contain a web decoration. Many spiders occasionally failed to decorate their webs, but only five animals (9.1%) never built a web decoration at all during the observation period.

Web size.—The spiders more than doubled the catching area of their webs within the 30 day observation period. The mean size of the first web we measured was 635.30 ± 44.46 SE cm² ($n = 55$) and the mean size of the last measured web was 1630.61 ± 21.99 SE cm² ($n = 55$). Over the whole observation period, undecorated webs were significantly larger than decorated webs, ranging from 625.21 ± 56.88 SE cm² to 646.54 ± 70.57 SE cm² at the beginning of to the experiment to between 1563.21 ± 42.56 SE cm² and 1700.50 ± 37.42 SE cm² at the end of the period (paired t -test: $t = 2.11$, $P < 0.05$). However, the mean decoration size did not significantly change over time, and ranged from 55.17 ± 72.72 SE mm² ($n = 55$) at the beginning to 46.25 ± 54.06 SE mm² ($n = 55$) at the end of the observation period (Pearson, $r^2 = 0.04$, $P = 0.29$). We found a significant positive correlation between spider size and web area (Pearson, $r^2 = 0.31$, $P < 0.01$; $n = 621$). In contrast, we found no significant correlation between spider size and web decoration size. Consequently, the size of the decorated web area in relation to the total web decreased over time.

Variation of web decorating behavior.—The variation in web decoration shapes was very high and the "typical" cruciate type was rarely constructed (Fig. 2); females of *A. keyserlingi* most often constructed single arm decorations ($n = 47$ spiders in 65.13%, $n = 282$ observations), and decorations with two ($n = 31$ spiders in 24.48%, $n = 106$ observations), three ($n = 10$ spiders in 5.54%, $n = 24$ observations), or four ($n = 15$ spiders in 4.85%, $n = 21$ observations) zig zag bands were less frequent. In all partial cross shapes (one to three arms), the bands were added to the lower web half significantly more often (85.2% vs. 14.8%, $n = 50$; $X^2 = 9.12$, $P < 0.01$). There

**Number of web decoration bands
(decorations, n=433)**

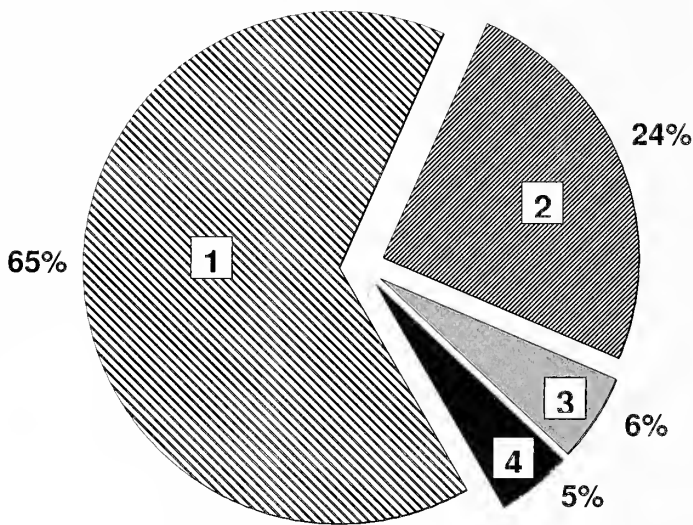


Figure 2.—The variation in web decoration patterns of *A. keyserlingi* females under laboratory conditions. Partial cross shapes (one to three decoration bands = number 1–3 in the diagram) are more frequent than the typical cruciate shape (number 4).

was also strong intra-individual variance; most spiders (65.45%, $n = 36$) altered the web decoration pattern up to four times over the observation period: Thirteen spiders (23.64%) altered their web decoration pattern once; nine (16.36%) altered the pattern twice; six individuals (10.51%) altered it three times; and three spiders (5.46%) altered the decoration four times. Only 19 spiders (with 34.55% significantly less, $X^2 = 9.55$, $P < 0.01$) constructed the same number of arms within the observation period and five individuals (9.09%) built no web decoration at all. These latter spiders also had a significantly lower web decorating frequency (new decoration every 3.7 ± 4 SE days) than individuals that constructed more variable shapes over time (new decoration every 1.5 ± 0.9 SE days, $n = 31$; t-test: $t = 2.91$, $P < 0.01$).

Web decorating behavior in the context of molting events.—Within the 30 day observation period 46 of 55 subadult spiders molted to maturity. Spiders suspended the two-day web building rhythm a few days before molting, and on average 3.3 ± 1.6 SE days elapsed between the “last” web building and the start of the molt. The mean interval between constructing the “last” web decoration prior to the final molt into sexual maturity (2.8 ± 1.5 SE days) was also longer than the mean decorating interval at other times (every 2.37 ± 0.37 SE day, see above). The molting events coincided with an increase in overall web size: the web size had increased by 19% (mean $+260$ cm²) in the ten day period after the molt (from 1080.37 ± 42.9 SE cm², $n = 101$ prior to the molt to 1340.36 ± 25.56 SE cm², $n = 205$; paired t-test: $t = -4.88$, $P < 0.01$). Ten spiders (22%) added a new web decoration to an old web prior to the molt. The change in web decorating and web building frequency was exclusively observed in combination with molting events, and the most conspicuous change was the dramatic increase in the web decoration size (Fig. 3) during the pre-molting phase (last subadult webs). The size of the

“regular” web decorations, both in penultimate webs before and in the first webs after the molt, were significantly smaller (68.78 ± 10.45 SE mm², $n = 43$ vs. 58.39 ± 9.24 SE mm², $n = 45$) than those constructed directly in the last web before molting (211.74 ± 35.94 SE mm², $n = 46$; ANOVA: $F = 14.36$, $P < 0.01$).

The “supersized” decorations of the molting webs were characterized by a partial loss of the typical zig zag look (Fig. 3, right). Moreover, these peculiar decoration bands overlapped in the hub region of the web, which was never observed in intermolt webs. Finally, only one individual molted in a web without a web decoration.

All in all, individuals of *A. keyserlingi* reduced their web building frequency (Fig. 4A) and increased the size of their web decorations prior to their final molt to sexual maturity (Fig. 4B).

DISCUSSION

Although individuals of *A. keyserlingi* usually build cruciate web decorations (Rao et al. 2007) consisting of up to four zig zag-shaped silk bands (Bruce 2006), we observed substantial individual variation in web construction and decorating behavior in *A. keyserlingi* in our study. Web size strongly correlated with the spider's size and larger females built larger webs. Moreover, we could confirm previous reports by Hauber (1998) and Craig et al. (2001) on a negative correlation between web size and decoration size. Undecorated *Argiope* webs were larger than decorated ones. Since we kept the feeding regime constant, this might indicate a tradeoff between web size and decoration as suggested by Craig et al. (2001).

Although web size was positively correlated with spider size, larger spiders did not build larger web decorations. Consequently, the relative decoration area of the web decreased over time, which may reflect previous reports of reduced web decorating behavior in later adult stages of *Argiope* spiders (Peters 1953; Edmunds 1986; Nentwig & Heimer 1987). The intra-individual variation in the shape of the decoration was remarkably high. Very few spiders consistently built only one particular pattern. An explanation for this may be given by the results of Craig et al. (2001) on *Argiope argentata* (Fabricius 1775). They argue that individual decoration patterns have a genetic component and any variation represents the influence of ecological conditions. Most spiders in our study alternated the web decoration type, some individuals up to four times. Although this high variation may have been affected by the laboratory conditions it has also been observed in many other *Argiope* species (e.g., Blackledge 1998 in *A. aurantia* Lucas 1833 and *A. trifasciata* (Forskål 1775); Hauber 1998 in *A. appensa* (Walckenaer 1842); Seah & Li 2002 in *A. versicolor* (Doleschall 1859); Bruce & Herberstein 2005 in *A. picta* L. Koch 1871 and *A. aetherea* (Walckenaer 1842)).

Argiope keyserlingi females in our study regularly rebuilt their orb webs every second day, and the web decorating frequency followed this rhythm. The only exceptions occurred on those days leading up to the commencement of the final molt to sexual maturity. During this time, some spiders added web decorations to their old webs. Typically, *Argiope* spiders do not rebuild orb webs several days before they molt to maturity (Robinson & Robinson 1978; Nentwig & Heimer

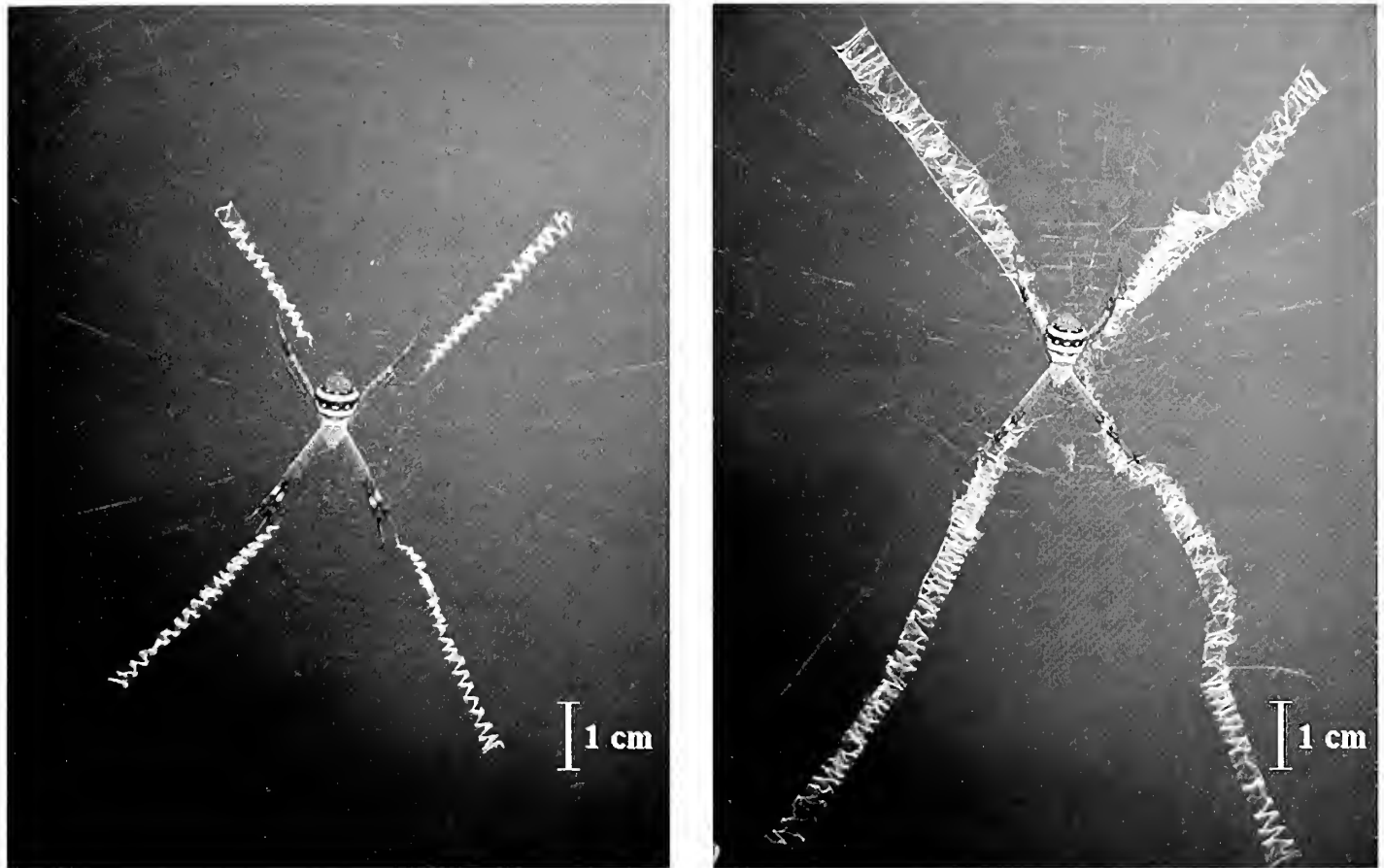


Figure 3.—The “regular” web decoration (left) and the “supersized” web decoration (right) of *A. keyserlingi*.

1987; Eberhard 1990). Robinson & Robinson (1973) suggest that a tradeoff between silk production and the biosynthetic efforts in preparation of the molt provides an adaptive explanation for this phenomenon. However, the frequency of web decorating prior to molting did not decline, despite the reduction in web building, because some spiders added new decorations to already existing, old, and dilapidated webs.

Indeed, the dramatically oversized decorations that spiders built prior to the molt (Fig. 4) were the most conspicuous difference to the intermolt webs of subadult and the webs of adult individuals. The phenomenon that spiders build more frequent and/or more perfect web decorations prior to the molt was already observed in *A. argentata* and *A. savignyi* Levi 1968 in the laboratory (Nentwig & Heimer 1987). Moreover, Edmunds (1986) noticed larger and denser decorations prior to moltings in a wild population of *A. flavipalpis* (Lucas 1858). These anecdotal reports, however, have never been empirically quantified. In our study we could show that web decorations in *A. keyserlingi* were three times larger shortly before the maturation molt and did not correspond with the individual variation in decoration shape. Decoration size decreased to the intermolt level immediately after the molt. Consequently, very large decorations were thus directly linked to the molting procedure.

Do our findings contribute to resolving the controversy over the adaptive significance of web decorations (see Bruce 2006)? Web decorations have been discussed in a variety of

contexts, including in the context of prey attraction (Herberstein 2000; Herberstein & Fleisch 2003; Li 2005). Although we cannot exclude this explanation for decorations in regular webs, the observed increase in web decorating activity in *A. keyserlingi* prior to the molt is not predicted by this hypothesis. Spiders decrease their foraging efforts during the pre-molt phases (Higgins 1990), presumably because there is little opportunity to consume food during molting. Nevertheless, web decorations may provide particular mechanical support for orb webs (Simon 1895) during the molting phase (Robinson & Robinson 1970, 1973, 1978; Nentwig & Heimer 1987). Higgins (1990) argued that the web decorations of *Nephila clavipes* (Linnaeus 1767) (Nephilidae) help prevent the spiders contacting the sticky spiral, which could interrupt the molting procedure by hindering individuals from freeing themselves from the old exoskeleton. Since molting events are generally vulnerable phases in the life of a spider (Robinson & Robinson 1973; Baba & Miyashita 2006) the potentially protective properties of web decorations may be relevant in preserving the integrity of the web during the molt (Horton 1980; Eisner & Nowicki 1983; Kerr 1993). Additionally, the potential protection against predators (Eberhard 1990; Schoener & Spiller 1992; Blackledge & Wenzel 2001) would also predict an increase in decorating investment because spiders are especially vulnerable to predators during the molt or shortly afterwards (Tanaka 1984; Baba & Miyashita 2006).

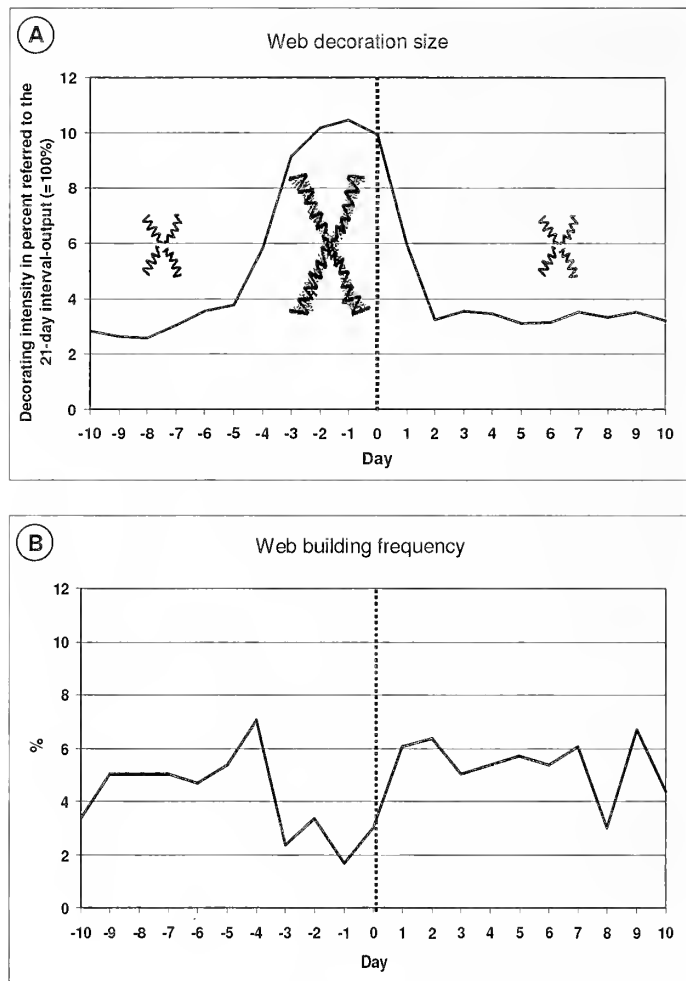


Figure 4.—A. The size of the web decoration of *A. keyserlingi* dramatically increases prior to the maturation molt and then returns to the level prior to the molting event; B. Web building frequency decreases prior to the last molt; dotted line: day of molting (= day 0).

Shortly after a molt spiders are vulnerable to desiccation due to the slowly sclerotizing exoskeleton. In this phase it must be particularly important to balance the hygric status through water ingestions. In this context (large) web decorations might be practical tools: some *Argiope* spiders directly ingest water from parts of their web decorations (Olive 1980; Walter et al. 2008a).

Since *Argiope* spiders can also successfully molt on webs without a web decoration (Nentwig 1986; own observations) the adaptive effects of the decorations may play a subsidiary role. Instead, the increase in web decoration investment may proximately derive from direct physiological processes, particularly since resource allocations directly influence interactions between molting, silk composition and web building behavior (Townley et al. 2006). Thus, it might be necessary to “outsource” a certain amount of nutrients for optimizing the molting procedure. Higgins & Rankin (2001) showed that “well-fed” individuals of the orb weaving spider *N. clavipes* more often suffer from molting failures when exceeding a critical pre-molt mass. They concluded that this might be the cost for the ability of rapid growth based on an almost non-limited food intake in this species. This may also

be relevant for the rapid growth of *Argiope* spiders. Outsourcing body mass in the form of silk proteins may ensure an “optimal” molt-weight. In this context it is possible that *N. clavipes* builds web decorations only shortly before a molt (Higgins 1990). Conversely, a molt is always combined with a loss of body mass (through the failure to consume exuvia) (Hutchinson et al. 1997), and outsourcing silk proteins may allow spiders to minimize nutrient waste.

The link between the increase of web decorating behavior and moltings might also be explained by a requirement to outsource specific, physiologically important compounds that would be otherwise metabolized during the molting procedure or the non-foraging days shortly before and after the molt. Such allocation occurs for different compounds in several spider species [e.g., choline, Higgins & Rankin 1999 for *N. clavipes* and Townley et al. 2006 for *Argiope trifasciata* and *A. aurantia*; GABamide, Townley & Tillinghast 1988 for *Araneus cavaticus* (Keyserling 1881)]. Perhaps the enlarged decoration simply provides a storage area for the silk proteins themselves. The aciniform decoration silk is also used for immobilizing prey (Peters 1993; Tso 2004). Thus, web decorating might be crucial for maintaining a certain level of activity in the aciniform glands for an optimal performance of *Argiope*’s typical “wrap attack” strategy of prey capture (Olive 1980; Tso 2004; Walter et al. 2008b). After molting, spiders must swiftly resume capturing prey to compensate for lost foraging opportunities of the previous days. For subsequent capture events, *Argiope* requires large amounts of wrapping silk that has to be newly synthesized after the molt. Since several types of silk glands are remodeled during a molt, they may not be fully operative in the days immediately after the molt (Townley et al. 2006). If this is also true for the *glandulae aciniformes*, the extensive web decorations may provide an ideal store of the crucial silk components, allowing the swift replenishment of the aciniform silk following molting. The highly efficient recycling of web parts (Peakall 1971) thereby clearly reduces the costs of silk production (Janetos 1982; Opell 1998) by reusing the relevant amino acids.

To confirm the physiological background of our observations, further studies should concentrate on the impact of different metabolic processes on the web decorating behavior prior to moltings, with a focus on those spiders that nonetheless molt without decorations. However, irrespective of the actual ultimate adaptive mechanisms of web decorations, it seems that these structures may play a more specific role in the molting web than in the regular capture web in *Argiope*. Given the large size of the molting decorations in contrast to relatively small and highly variable decorations in regular webs, it may well be that the clue to solving the riddle of these structures lies in the physiology of the molting spider.

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Ontogenetic changes in web architecture and growth rate of *Tengella radiata* (Araneae, Tengellidae)

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Abstract. In some spiders features of the webs of early instars may represent features of the ancestor's web. Some second instar spiderlings (first instar outside of the egg sac) of *Tengella radiata* (Kulczynski 1909) construct a small sheet web without any type of retreat. In subsequent instars, spiderlings construct webs that consist of a sheet with a small retreat that opens near its center. Webs gradually change as spiderlings grow and webs of 7th instar spiders are indistinguishable from those of adult females. Spiders only begin to include cribellate threads in their webs during the 7th instar. The growth of *T. radiata* is slow during the first three instars, but spiders' sizes increase steadily in the subsequent stages. Legs I of adult males are longer than in females, indicating an allometric growth that occurred mainly during the last molt of males.

Keywords: Spiderlings' webs, cribellate silk, cephalothorax and leg growth

Little is known about ontogenetic changes in most spiders' webs, particularly in non-orb weavers (Eberhard 1990). The first webs constructed by newly emerged spiderlings (second instar spiderlings) in several spider families differ from the webs of adults and they tend to represent less derived stages or characters compared to the features of the webs of adult spiders (Nielsen 1931; Eberhard 1977, 1985, 1986, 1990; Robinson & Lubin 1979). Some of these differences might also be related to underdevelopment of silk glands, as is the case in *Uloborus diversus* Marx 1898 (Eberhard 1977). Webs constructed by young spiderlings of this species lack cribellate silk, and radial threads are more numerous than in webs of adult spiders. Another possible difference in young spiderlings' webs may also be related with the type and size of prey that spiderlings can handle (Lubin 1986).

Webs of young cribellate and non-cribellate spiderlings have been studied in Orbiculariae orb-weaving spiders (Eberhard 1977, 1985, 1986). In some of these spiders in which architecture of adult webs depart from a typical orbicular web (Eberhard 1985, 1986), the webs of newly emerged spiderlings are orbicular, indicating that their ancestors probably possessed orbicular webs. A similar pattern is showed by cribellate and non-cribellate non-orb weavers such as the psechrid *Fecenia* sp. (Robinson & Lubin 1979) and some theridiid species (Nielsen 1931; Szlep 1965).

In this study, we focus on the cribellate spider *Tengella radiata* (Kulczynski 1909), a species of Tengellidae that builds funnel webs and is restricted to Costa Rica (Eberhard et al. 1993). Its web is regularly inhabited by some symbiont spiders (e.g., *Philoponella* sp., *Mysmenopsis* spp.) and plokiophilid bugs (e.g., *Lipokophila* spp.) (Eberhard et al. 1993). The structure and production of the cribellate threads of this spider have been described and compared with threads of other cribellate spiders (Eberhard 1988; Eberhard & Pereira 1993). The courtship and copulation have also been reported and compared with those of other spiders in related families (Barrantes 2008), and Santana et al. (1990) investigated the predation rate in the field and estimated the metabolic rate of this spider. Other than this reported work, there have been no

published studies on the ontogenetic changes in the funnel, cribellate web, or on the growth of this spider.

If there are ontogenetic changes in webs, we expect there to be transitional stages between the first webs and the adult webs. We describe here the architecture of the adult web and changes in the web architecture that occur between the immature stages of *Tengella radiata*. We also describe the number of molts, growth, and feeding behavior of spiderlings for this spider.

METHODS

We observed ($n > 30$) and photographed ($n = 5$) webs of wild mature females of *T. radiata* in San Antonio, Escazú, San José province (= SAE; 10°56'N, 84°08'W) and used this information to describe the adult web. The egg stage period and maternal behavior were described from a female raised from eggs in captivity and maintained in a plastic box (30 × 18 × 11 cm) where she constructed her web.

In order to rear and study numerous spiderlings we collected egg sacs from two mature female from two localities. One was from an adult female in SAE and a second from a female from La Selva Biological Station (= LSBS; 10°26'N, 83°59'W), Organization for Tropical Studies, Heredia province, Costa Rica. Each egg sac was placed on a mass of dry cotton inside a plastic container (13 × 13 × 6 cm) with a little piece of humid cotton at a corner. All containers were maintained indoors at a temperature of 18–20° C. From one egg sac (SAE), 16 spiderlings were separated as they emerged and each one was maintained individually in a plastic container (13 × 13 × 6 cm); some of these spiderlings were placed in a larger container (30 × 15 × 10 cm) when they reached their seventh instar. Webs of some of these 16 individuals were photographed and their shed cuticles measured at each stage (details described below) to describe the ontogenetic changes in the web and the growth of this spider. From a second egg sac (LSBS) we separated three groups of 10 spiderlings and each group was maintained in a container (13 × 13 × 6 cm). Feeding behavior was observed in these groups of spiderlings. (Spiderlings from the second egg sac were released to the wild as they molted the third time as were those remaining spiderlings from the first egg sac). We consider spiderlings that recently emerged from the egg sac as second instar individuals (Foelix 1996).

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The plastic container of each of the 16 spiderlings kept individually had four small rocks, whose base and height varying from 2 to 3 cm. One rolled dry leaf, forming a cone of ca 2 cm with an opening of ca 0.5 cm in diameter, was attached to one of the rocks with masking tape; rocks were all fastened to the bottom of the container. This "rock landscape" was fashioned to offer spiderlings enough supports to construct their webs, and the rolled leaf was offered as a "natural tunnel." Two to four webs constructed by spiderlings from 3rd to 6th instars were lightly coated with cornstarch and then photographed. The longest and widest sides of these, approximately rectangular webs were measured. Spiderlings of the photographed webs were collected and preserved in alcohol to avoid possible effects of cornstarch in the construction of subsequent webs. The web of the second instar spiderlings was sketched using photos and observations under the dissecting microscope; cornstarch adhered to threads of these webs was insufficient to allow good contrast photographs.

We measured the length of tibiae and femora of legs I and IV, and the length and width of the cephalothorax in shed cuticles of the different stages of those 16 spiders maintained individually in containers, three adult males, and three adult females to estimate the spiders' growth between stages (2nd instar to adult stage). Sample sizes were not the same for each stage because some spiderlings were collected and some shed cuticles were destroyed when we withdrew them from the web, and tibiae in all second stage cuticles collapsed and were impossible to measure. To calculate the percentage of growth between subsequent stages, we subtracted the length of a particular structure to the mean of that structure of the previous stage (M_{ps}), then divided this difference between M_{ps} ,

and multiplied this proportion by 100 (e.g., $[FI_{21} - MFI_1]/MFI_1 * 100$; FI_{21} - femur I from individual 1 of second instar, MFI_1 - mean of femur of all individuals of instar 1). We used a digital camera (Nikon, Coolpix 4500) to photograph each femur, tibia, and cephalothorax under a dissecting microscope, and measured them using the software program Image Tool v. 3.0. Four 3rd instar spiderlings were observed under the dissecting microscope to check for the presence of the cribellar plate and calamistrum.

During the 2nd and 3rd instars, spiderlings were offered a *Drosophila* fly every other day, 4th instar spiderlings were offered two *Drosophila* flies every other day, and spiderlings of later instars were offered one blow fly (Calliphoridae) or a moth every three days. All containers had a small piece of wet cotton for the spiderlings to drink. Feeding behavior observations were made on both solitary spiderlings and on those maintained in groups. Additional behavioral observations of adults and spiderlings were obtained from adult spiders raised from eggs in captivity and complemented with the field information from SAE and LSBS. Voucher specimens of spiders from all stages were deposited in the Museo de Zoología of the Universidad de Costa Rica, San José.

RESULTS

Adult web.—The adult web of *T. radiata* consists of a large, more or less triangular, horizontal sheet with a dispersed tangle above and beneath it (Fig. 1; Eberhard et al. 1993). It is usually built near a large object such as rock or a tree trunk. At the "interior," most protected section (the apex) of the web the spider constructs a tunnel that varies between 5 and 20 cm long ($n = 20$). The spider rests at the mouth of the tunnel or inside it during the day. At night ($n = 10$) the spider usually

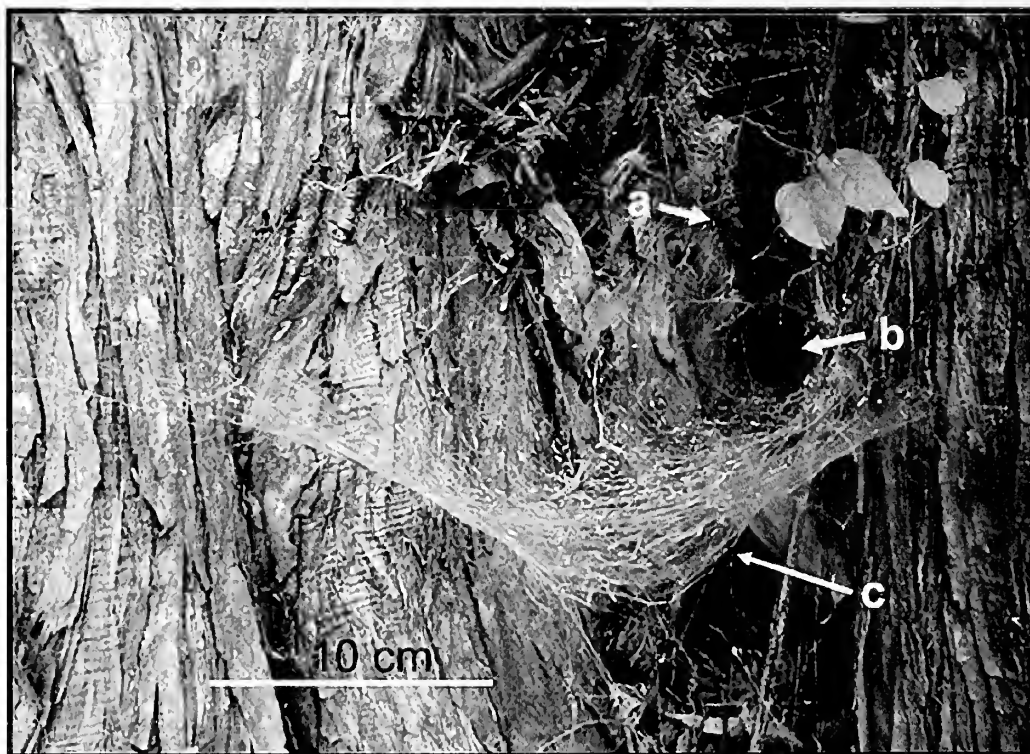


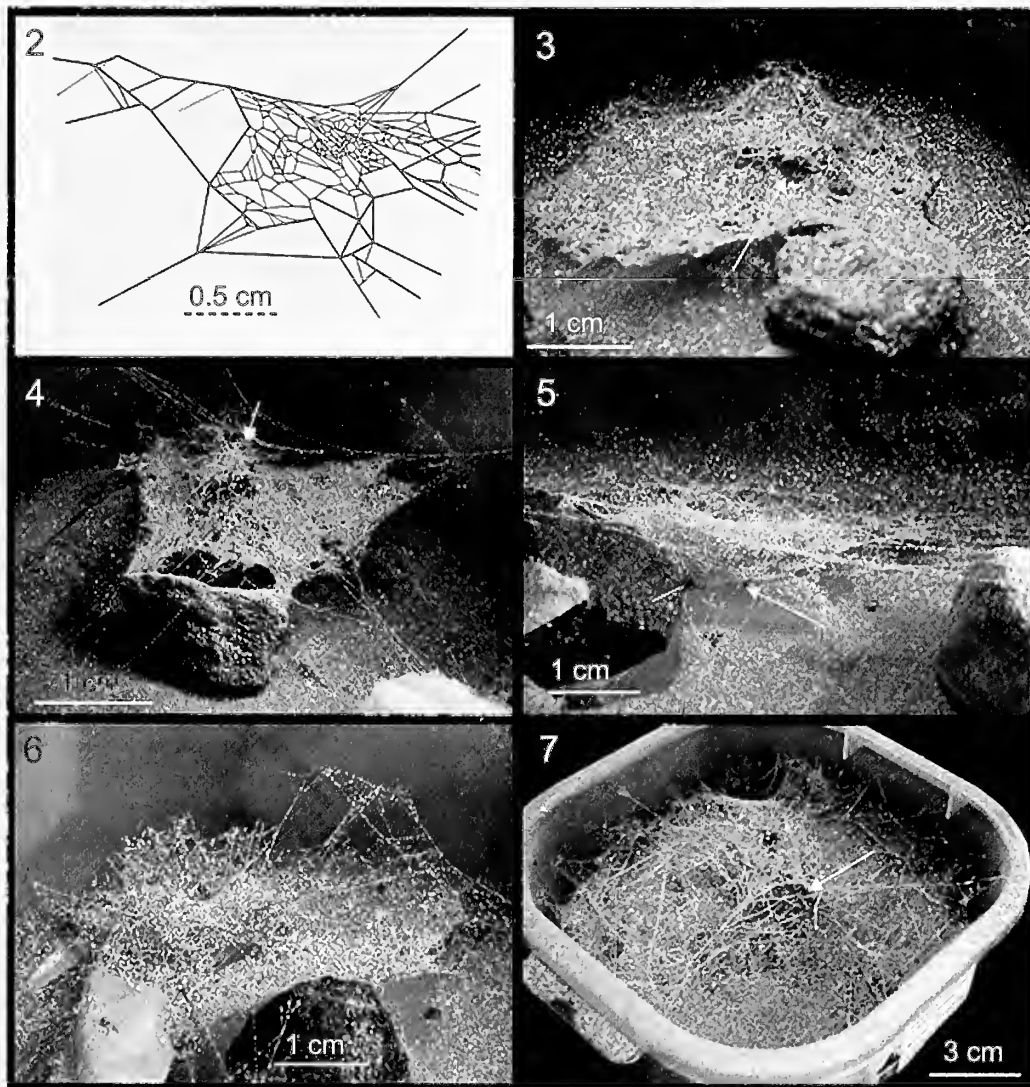
Figure 1.—Frontal view of an adult web of *T. radiata* (without cornstarch): a. Threads of the upper tangle. b. Tunnel at the "interior" section of the sheet. c. Sheet.

rests at the mouth of the tunnel, but is often observed repairing the web or producing adhesive cribellate threads that she lays on the sheet and upper tangle. Newly constructed webs frequently lack cribellate threads, but this silk accumulates on the sheet and upper tangle over time, until the web collapses apparently due to the weight of debris accumulated on its sheet. Adult males ($n = 3$) did not build webs when placed in a large plastic container. However, they killed and fed on prey that walked nearby. Females ($n = 5$) placed in similar containers built a complete web.

Duration of egg stage and maternal care.—One spider produced two egg sacs in captivity, the first 32 and the second 48 days after copulating. Spiderlings emerged from the first egg sac 58 days later; no spiderlings emerged from the second egg sac. The egg sacs were attached to the roof of the tunnel, as were five egg sacs observed in the field. In captivity, the spider added some small pieces of prey cuticle to the external surface of the egg sacs; egg sacs observed in the field were also covered with detritus. The female spent most of her time

(except when capturing prey and feeding) hanging from the tunnel with her legs and palps surrounding the egg sac. Nearly the entire time, she contacted the egg sac with legs II and III (less frequently with legs IV), and her palps. Occasionally, she stood on the bottom of the tunnel, with one of her legs (usually one leg III) raised to contact the egg sac. When the spider produced the second egg sac, she concentrated her care on the second sac. The spider died after living for 18 months and 20 days (from emergence through adulthood).

Ontogenetic changes in webs.—During the second instar, 4 of the 16 spiderlings used the tunnels (rolled leaf provided) but did not construct webs, 8 remained under a rock, and 4 constructed a web that consisted of a small, more or less rectangular, sheet (Fig. 2). At first the web consisted only of more or less horizontal threads that extended between rocks or between rocks and the container wall. The horizontal threads were about 1.5 cm above the container floor and other threads connected them to the floor and to the container wall above. These threads were part of the scaffolding that supported the



Figures 2–7.—Webs of early stages of *T. radiata* (with cornstarch): 2. Molting web of second stage spiderlings; 3. Type I web of third stage spiderling; 4. Type II web of third stage spiderling; 5. Web of fourth stage spiderling; 6. Web of fifth stage spiderling; 7. Web of seventh stage spiderling. White arrows in Figures 3, 4, 5, and 7 show the tunnel opening. The right tip of the short white line in Figure 5 shows the spiderling inside the retreat.

rest of the web. During the next days the spiderlings constructed a dense sheet of very fine threads. The angle of the sheet varied from nearly horizontal to about 15° (angles were visually estimated). The complete web was constructed over the first 2 to 4 days. When the web was finished, the spiderling remained motionless, near the center, and on top of the sheet until its next molt. These webs all lacked tunnels or any other type of retreat. During this stage, which lasted 11.3 days ($SD = 0.4$) spiderlings did not feed; they did not react to the presence of prey on their webs.

The third-stage spiderlings ($n = 16$) constructed two types of webs. The most common type (13 out of 16) was a small (range = $3-4 \times 2-2.5$ cm) dense, more or less horizontal sheet with a resting place (retreat) that was constructed nearly perpendicularly under the sheet (type I) (Fig. 3). This retreat was a small bag of loose silk with the exit near the center of the sheet (Fig. 3). The other web (type II) was also a flat sheet, but with the bag-like retreat constructed on the sheet forming a small roof, with a relatively dense tangle above the sheet (Fig. 4). Threads of the tangle served as support for the much finer threads of the sheet and retreat. All spiderlings in this stage captured *Drosophila* flies dropped on the sheet.

The webs of fourth-stage spiderlings were in general larger (range = $5-6 \times 3-3.5$ cm) than those of the previous stage. Spiderlings expanded the sheet and retreat of the web constructed in the previous stage, and constructed a tunnel under the sheet. The closed end of the tunnel nearly reached one border of the sheet (Fig. 5), and spiderlings rested deep inside the tunnel (Fig. 5). The general shape of these webs was similar to webs of the previous instar and type I and II webs were still distinguishable. Webs of fifth and sixth stages were similar in the general features but larger compared to webs of the previous stage (Fig. 6).

Seventh-stage juveniles constructed a much denser tangle above the level of the sheet. In this stage the tunnel of two webs ($n = 9$) was constructed on the sheet for most of its length, with its opening near the center of the sheet. The furthest end of the tunnel curved down and under the sheet, similar to a type II design (Fig. 7). The other seven webs were similar to the adult webs, with the opening of the tunnel at one extreme of the sheet. This was the first stage in which cribellate threads were observed on the sheet and upper tangle of the web (Fig. 8), though the cribellar plate and calamistrum were already present in 3rd instar spiderlings. The web of older stages (in larger containers) was indistinguishable from webs of adult spiders.

Spiderling feeding behavior.—Third and fourth instar spiderlings attacked by rushing onto the sheet to the prey and biting it. If prey was small, relative to the spiderling size, the spiderling fed on the prey without releasing it. If prey was large, it was released by the spiderling as soon as the prey's struggling stopped, returning to feed on it a few seconds later. One fourth instar spiderling (in a group of 10) wrapped the prey after biting it. The spiderling released the prey as it stopped struggling and nearly immediately began to wrap it. During wrapping, the spiderling turned in place while attaching wrapping lines to the substrate (the sheet). The wrapping movements were similar to those described for adult spiders (Barrantes & Eberhard 2007). Another spiderling approached a large blow fly (larger than a house fly) slowly. The spiderling backed away as the fly struggled and then cut

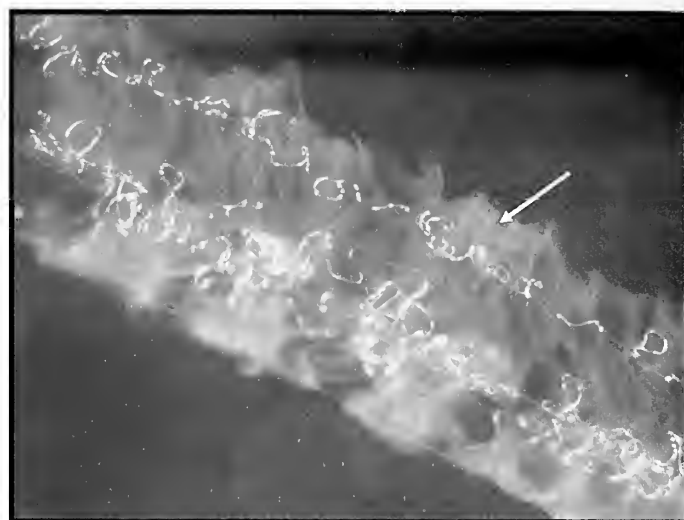


Figure 8.—Cribellate threads (white arrow) from webs of seventh stage spiderlings.

some sheet threads and walked, hanging under the sheet to the prey and bit one of the fly's legs through the sheet. Neither wrapping nor attacks from under the sheet were observed in any fifth instar individuals. Older juvenile spiders (sixth or older instars) always moved on the upper surface of the sheet, and often wrapped large prey (e.g., moths and large flies), with movements similar to those of adult spiders (Barrantes & Eberhard 2007). Large prey were carried inside the tunnel by 7th stage, subadult, and adult spiders, and their carcasses were left inside the tunnel.

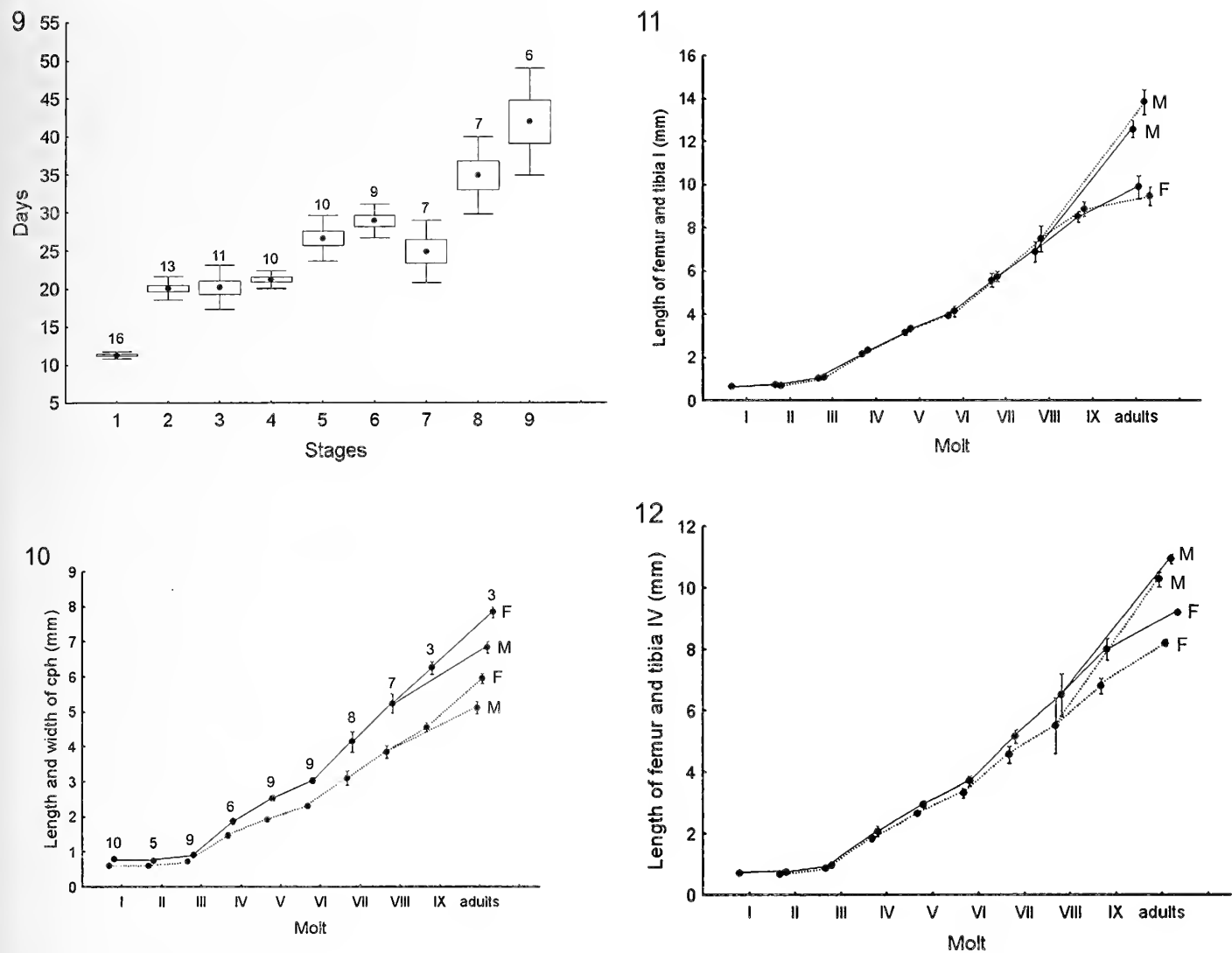
Additional behavioral observations.—Early instar spiders did not molt at any consistent site in the web ($n > 50$). However, older stages (7th to pre-adult) molted inside the tunnel but they carried the shed skin to the farthest extreme of the web ($n = 9$).

Number of molts and growth.—The males had eight molts ($n = 4$) and the females nine ($n = 4$) to attain their adult stages. The mean time from emergence from the egg to the eighth molt was 186.7 days (± 10.5), when males molted to the adult stage. Females lasted 42 days (± 7) more to their next and last molt (Fig. 9).

The general pattern of growth of the cephalothorax (width and length) and legs I and IV (tibia and femur) were similar. In the three first stages these structures grew very little, but during the following stages the size of the cephalothorax and legs increased steadily (Figs. 10–12). In fact, the growth of all morphological features was proportionally much larger between the third and the fourth stage, than between other subsequent stages (Table 1). It is also evident that the length of the cephalothorax increased faster than its width (Fig. 10), indicating an allometric growth of the length relative to the width of the cephalothorax. In addition, legs of adult males were also notably longer than those of adult females, despite the additional molt of females.

DISCUSSION

The architecture of the webs of *T. radiata* changes as spiders mature. The first web constructed by 2nd instar spiderlings, which have recently emerged from the egg sac, apparently serves as a molting place, since spiderlings in this stage did not capture prey. In nature and in captivity the second instar spiderlings construct a communal molting web inside the



Figures 9–12.—Inter-molt time and growth of *T. radiata*: 9. Intermolt time (mean, standard error and standard deviation) from the first to the ninth stage out of the egg sac; sample size above each stage mean; 10. Mean and standard deviation of the length (solid line) and width (dotted line) of cephalothorax (cph); sample size above each mean, F and M indicate the values for adult females and adult males respectively; 11. Mean and standard deviation of the length of femur (solid line) and tibia (dotted line) of leg I; 12. Mean and standard deviation of the length of femur (solid line) and tibia (dotted line) of leg IV.

tunnel of their mother’s web, and only begin to abandon the tunnel and the web after they molt to the third instar (GB unpublished data).

Both of the two types of webs constructed by third through sixth instar spiderlings had retreats that opened near the center of the sheet (Figs. 3–7). If, as in other groups, the webs of early instars represent less derived characters than those of the adult

web (Eberhard 1986, 1990), the ancestral web of *Tengella* might have been a sheet with a tunnel retreat extending below its center. However, comparative data of closely related species (Coddington 2005) are required to test this hypothesis.

The lack of cribellate threads on the sheet of juvenile spiders (2nd to 6th instar) may either represent an ancestral condition, an undeveloped condition of the cribellum

Table 1.—Percentage of growth of the width and length of the cephalothorax (cph) and the femur (F) and tibia (T) of legs I and IV between successive stages (first row). Sample size in parentheses beside or under the stage codes.

	I to II (5)	II to III (9)	III to IV (6)	IV to V (9)	V to VI (9)	VI to VII (8)	VII to VIII (7)	VIII to IX (6)	VIII to ♂ (3)	IX to ♀ (3)
Cph W	0.6 ± 9.9	19.9 ± 1.9	104.4 ± 11.7	30.7 ± 2.9	19.8 ± 4.3	35.3 ± 8.7	23.9 ± 5.8	18.6 ± 3.5	32.9 ± 4.7	30.5 ± 3.3
Cph L	0.1 ± 0.2	21.6 ± 3.3	106.4 ± 9.2	35.6 ± 4.4	20.1 ± 3.7	36.6 ± 9.7	26.5 ± 6.4	19.3 ± 3.4	30.5 ± 3.2	25.3 ± 2.6
FI	21.4 ± 5.2	41.0 ± 3.9	104.4 ± 14.6	46.5 ± 5.5	22.4 ± 9.8	42.0 ± 8.4	23.8 ± 8.7	23.7 ± 3.7	82.4 ± 5.9	15.8 ± 6.5
Tbl		56.6 ± 5.6	114.5 ± 8.0	41.8 ± 7.3	24.4 ± 8.1	38.9 ± 5.9	30.6 ± 10.8	18.5 ± 4.5	84.8 ± 7.7	18.3 ± 7.1
FIV	5.9 ± 3.3	32.3 ± 4.0	110.9 ± 17.2	42.0 ± 5.0	26.2 ± 5.5	38.7 ± 6.0	26.3 ± 13.3	22.8 ± 5.3	67.8 ± 2.6	14.2 ± 1.4
TblV		29.6 ± 5.5	109.5 ± 13.3	44.0 ± 4.2	25.1 ± 5.5	37.5 ± 8.3	26.3 ± 11.1	23.1 ± 4.7	86.3 ± 4.3	20.2 ± 2.0

apparatus, or both. The presence of the cribellum and calamistrum in third instar spiderlings but the lack of cribellate silk on their webs, indicate that these structures may not be functional in the early stages of *T. radiata*, as occur in some uloborids (Eberhard 1977; Opell 1982), or that the high demand of energy involved in drawing the cribellar fibrils (Eberhard 1988) prevent young spiderlings from using this type of silk.

The lack of cribellate silk in early stages and newly constructed webs of adult *T. radiata* did not prevent spiders from using their webs to capture prey, though cribellate silk possibly restrain and reduce movements of prey on the web. Spiderlings at early stages showed attack and wrapping behaviors similar to those of adult spiders (Barrantes & Eberhard 2007). The wrapping behavior of spiderlings only differed from that of adults in that spiderlings did not hold the prey while wrapping it as adults do (Barrantes & Eberhard 2007). In addition, one spiderling attacked a large prey from under the sheet. This attack is apparently restricted to early spiderling stages, as it has not been observed in either large juveniles or adult spiders. The low frequency of occurrence of this behavior is unclear since attacking a large prey from under the sheet provides some protection to the spiderling as the sheet restrains the struggling prey and reduces the force of its movements (Robinson 1975; Lubin 1980).

In general the growth of *T. radiata* is slow, as expected from its apparently extremely low metabolic rate (Santana et al. 1990). Growth was very slow during the earliest stages (Figs. 10–12), but the relative increment in cephalothorax and leg size was more than 100% between the third and fourth stage. After the fourth stage, the cephalothorax and legs increased steadily with each subsequent molt, though the intermolt period tended to increase with each stage. This possibly indicates the need for more energy and time for growth and development of internal organs as spiders mature. Length of legs I and IV is nearly the same until the fourth instar. However, in the following stages, increments in the length of leg I are larger than in leg IV, possibly reflecting the different functions of these legs in young and adult spiders. For example, the tactile function of legs I likely favor their longer length (Foelix 1996).

The comparatively longer legs of adult males result from the allometric growth that occurred mainly during the last molt of males, as happens in wolf spiders (Framenau 2005). Though experimental evidence is lacking, field observations (e.g., males observed near or on females' webs) indicate that adult males abandon their webs to find receptive females, so that longer legs may result in greater step size to bridge gaps. If a more efficient search for females lead to a higher reproductive success in males, it is likely that longer legs in males evolved, at least partially, through indirect male-male sexual competition (Anderson 1994; Framenau 2005). Additionally, natural selection might have also favored longer legs in males, if such a trait allows them to run faster to escape from predators and from females during courtship, and provides them a greater sensory range (Gertsch 1949; Framenau 2005). Accordingly, the larger size of adult females' cephalothorax correlates with their larger body which is related to their capacity to produce large numbers of eggs (Gertsch 1949).

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Does the microarchitecture of Mexican dry forest foliage influence spider distribution?

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Abstract. Spider species diversity has been associated with vegetation structure and stratification but there are few studies comparing the spider distribution in different shrubs and trees. In this study we analyzed the species distribution of the spider community of 11 shrub and tree species in two different study sites in a Mexican tropical dry forest. We present results from multivariate analyses that explain their distribution. A classification analysis based on spider abundances separated one shrub, *Croton ciliatoglanduliferus*, from the rest of the plant species. This was explained by the presence of large numbers of the oxyopid *Peucetia viridans* (Hentz 1832) on this plant. A second cluster segregated broad-leaved from small-leaved, bipinnate species. This was mainly due to higher spider abundances in the latter type of plants. Four vegetation variables were estimated and their influence on the species distribution was assessed by means of a principal components and regression analysis. With the exception of *P. viridans*, all spiders were positively associated with number of leaves and number of branchlets per 50 cm branch and negatively with foliage area.

Keywords: Community ecology, species abundances, plant structure

Habitat structure is an important factor that influences diversity, abundance, and distribution of spider species (Lubin 1978; Hatley & MacMahon 1980; Evans 1997; Whitmore et al. 2002). The available evidence has been gathered from both natural communities (e.g., Lubin 1978; Robinson 1981; Raizer & Amaral 2001) and agricultural systems (Rypstra et al. 1999; Samu et al. 1999). Habitat structure and complexity are related to factors such as prey abundance, shelter against enemies and suitable microclimatic conditions (Riechert & Tracy 1975; Gunnarsson 1996; Halaj et al. 1998; Raizer & Amaral 2001). Habitat preferences, however, can be highly specific and species belonging to different guilds have particular requirements according to their morphological, physiological, and behavioral features (Turnbull 1973; Wise 1993).

Variation in plant height, foliage density, leaf surface area, number of leaves and branchlets, and number and type of inflorescences, can affect the abundance and distribution of foliage-dwelling spiders (Hatley & MacMahon 1980; Evans 1997; Halaj et al. 1998; Uetz et al. 1999; Raizer & Amaral 2001; Corcuera et al. 2004; Heikkinen & MacMahon 2004; Souza & Martins 2004, 2005). In this study, we evaluated the influence of plant architecture on the spider community by means of multivariate and regression analyses. We analyzed the abundance of foliage spiders and four plant attributes of 11 of the most abundant trees and shrubs found in a tropical dry forest in western Mexico.

Information on Mexican spiders is widely dispersed. After extensive bibliographical research, Jiménez (1996) found 7,916 species. It is not known how many specimens were collected from foliage since most studies were concerned with taxonomy (Jiménez 1996). There have been a few reports on foliage spiders on cacao and coffee plantations (Ibarra Núñez et al. 1995, 1997; Moreno-Molina et al. 2001; Pinkus-Rendón et al. 2006), but these studies concentrate on species richness and diversity. Besides a diversity analysis (Corcuera et al. 2004), to our knowledge nothing has been written on the distribution of foliage spider communities in dry forests.

METHODS

Study sites.—Tropical dry forests cover 42% of the tropical and subtropical land area on the planet (Murphy & Lugo 1986). The dominant plant species are strongly drought deciduous (Mooney et al. 1989). In Mexico, they are the prevailing vegetation type along the west coast and cover ca. 12.4% of the country's area (Arizmendi et al. 1990). Mexican tropical dry forests are found between 0 and 1990 m elevation (Rzedowski 1978). Mean annual temperature ranges from 20 to 29°C, and mean annual precipitation from 300 to 1800 mm (Rzedowski 1978). Dry forests are strongly seasonal, with a long dry season and intense rainy season (Rzedowski 1978; Murphy & Lugo 1986).

The study sites are located in the Municipality of Villa Corona in the state of Jalisco (20°20'N, 103°35'W). Altitude above sea level is 1640 m. Mean annual temperature was 20.3°C and mean annual precipitation from the last 15 years was 826 mm. Most of the rain falls between mid-June to mid-September and there are between 6 and 8 dry months each year.

Plant variables.—Eleven trees and shrubs were sampled in two sites (El Caracol and Charco Verde) to test the effect of plant architecture on the distribution of foliage spiders: *Bursera schlechtendalii*, *B. bipinnata*, *Guazuma ulmifolia*, *Heliocarpus appendiculatus*, *Ipomoea wolcottiana*, *Prosopis juliflora*, *Mimosa galeotti*, *Lysiloma acapulcense*, *Croton ciliatoglanduliferus*, *Acacia cymbispina*, and *Byrsonima* sp. (Table 1). These plant species are typical of Mexican dry and thorn forests and were the most common shrubs and trees in the study sites (Table 2). Details about plant cover estimation are given elsewhere (Corcuera & Butterfield 1999; Corcuera & Zavala-Hurtado 2006).

Foliage area, number of leaves and number of branchlets (i.e., small branches) were determined for each plant species. The sample unit was a 50 cm terminal branch from a limb rising horizontally from the center of the plant (McCaffrey et al. 1984). Foliage area was measured by drawing the contour

Table 1.—Mean (\pm SD, $n = 10$ per species) of plant height, foliage area, number of leaves and branchlets on a 50 cm terminal branch ($n = 3$ per species) for 11 species in two dry forest sites, El Caracol and Charco Verde, in the Municipality of Villa Corona, Jalisco, Mexico. * = small-leaved species.

Plant species	Code	Plant height (m)	Foliage area (cm ²)	Number of leaves	Number of branchlets
<i>Bursera schlechtendalii</i>	Busc	3.4 (0.32)	850 (386.1)	70.0 (28.28)	22.5 (6.4)
<i>Bursera bipinnata</i> *	Bubi	3.4 (0.71)	541 (140.3)	2473.2 (2692.16)	22.0 (9.9)
<i>Croton ciliatoglanduliferus</i>	Crci	1.1 (0.32)	1026 (631.8)	28.0 (16.17)	9.0 (4.2)
<i>Guazuma ulmifolia</i>	Guul	4.8 (0.98)	3349 (989.7)	45.8 (19.30)	21.5 (0.7)
<i>Acacia cymbispina</i> *	Accy	3.3 (0.71)	120 (27.6)	10670.4 (2313.43)	10.5 (4.9)
<i>Prosopis juliflora</i> *	Prju	3.9 (1.25)	242 (105.1)	6696.0 (2136.01)	11.0 (0.7)
<i>Byrsonima</i> sp.	Bysp	2.7 (0.70)	1712 (1065.1)	64.5 (21.71)	15.0 (4.2)
<i>Ipomoea wolcottiana</i>	Ipwo	5.0 (0.72)	2556 (960.2)	12.2 (7.79)	11.0 (2.1)
<i>Heliocarpus appendiculatus</i>	Heap	5.3 (0.67)	2050 (975.0)	15.0 (7.53)	8.0 (1.4)
<i>Lysiloma acapulcense</i> *	Lysp	4.4 (0.47)	340 (105.9)	30240.0 (11671.35)	11.5 (3.5)
<i>Mimosa galeotti</i> *	Miga	2.7 (0.48)	320 (209.6)	16301.0 (5250.44)	11.5 (7.8)

of all leaves present on the branch on millimetric paper with 1 mm divisions. The procedure was repeated on three branches for each species and the mean area (cm²) per branch was calculated. Mean number of leaves, or leaflets for bipinnate species, and branchlets per branch was obtained from the three samples of each species. Plant height was recorded in a sample of 10 individuals for each species. All plant variables were averaged from measures from both sites.

Spiders.—Spiders were collected by branch beating (Southwood 1978) in June, July, September, October, and November 1999, and January and April 2000. For each plant species, a terminal branch was chosen and beaten 10 times with a cane (trial samplings showed that more strokes did not dislodge more specimens) (Southwood 1978; McCaffrey et al. 1984). This procedure was repeated on 10 individuals of each plant species in each of the seven visits to each site. The specimens were collected in 60 cm diameter muslin covered trays. Two persons collected the spiders from the canvas using tweezers and manual aspirators. McCaffrey et al. (1984) found that this technique efficiently sampled the arachnafauna of foliage dwelling spiders. The number of individuals for each spider species (11 plants \times 7 dates) was added in order to execute the analyses, and the results were log transformed to obtain a normal distribution. The specimens were preserved in 70% alcohol and identified later at the Centro de Investigaciones

Biológicas (CIBNOR) in La Paz, Baja California. Voucher specimens have been deposited in the collection at the Laboratorio de Ecología Animal, UAM-Iztapalapa, México City.

Multivariate analyses.—We analyzed the spider community similarities with a classification using an unweighted pair group average method with percent similarity. A Principal Components Analysis (PCA) was used to analyze the distribution of spider species in relation to the plant species. Regressions were used to assess the relationship between the main PCA axes and the plant variables. The classification and ordination analyses were carried out using the statistical software MVSP 3.2 (Multivariate Statistical Package; Kovach 1999).

RESULTS

Plant variables.—Foliage area was greater for broad-leaved trees. *G. ulmifolia* had the largest area (3349 cm²), followed by *I. wolcottiana* (2556 cm²), and *H. appendiculatus* (2050 cm²). *Croton ciliatoglanduliferus* and *Byrsonima* sp. had intermediate foliage areas (1026 cm² and 1712 cm², respectively); both are broad-leaved shrubs. All small-leaved species had much lower foliage areas (Table 1).

Lysiloma acapulcense and *M. galleotti*, small-leaved species, had the highest mean number of leaves per terminal branch

Table 2.—Plant cover percentage and spider abundance and richness of 11 trees and shrub species in two dry forest sites, El Caracol (C) and Charco Verde (V), in the Municipality of Villa Corona, Jalisco, Mexico. * = small-leaved species.

Species	Plant cover (%)		Spider abundance		Spider richness	
	C	V	C	V	C	V
<i>Bursera schlechtendalii</i>	0.6	2.7	49	31	9	9
<i>Bursera bipinnata</i> *	2.9	3.3	68	84	11	11
<i>Croton ciliatoglanduliferus</i>	9.9	0.8	87	83	11	6
<i>Guazuma ulmifolia</i>	2.3	5.4	28	29	7	11
<i>Acacia cymbispina</i> *	31.1	23.2	128	108	12	9
<i>Prosopis juliflora</i> *	4.8	0.5	70	119	10	11
<i>Byrsonima</i> sp.	4.8	1.6	43	27	12	7
<i>Ipomoea wolcottiana</i>	16.0	6.0	35	35	8	8
<i>Heliocarpus appendiculatus</i>	1.9	7.9	32	45	10	6
<i>Lysiloma acapulcense</i> *	2.9	18.8	53	65	10	11
<i>Mimosa galeotti</i> *	11.6	4.9	74	47	11	10
Other plant species	11.1	24.8	—	—	—	—
Total	100	100	667	673	—	—

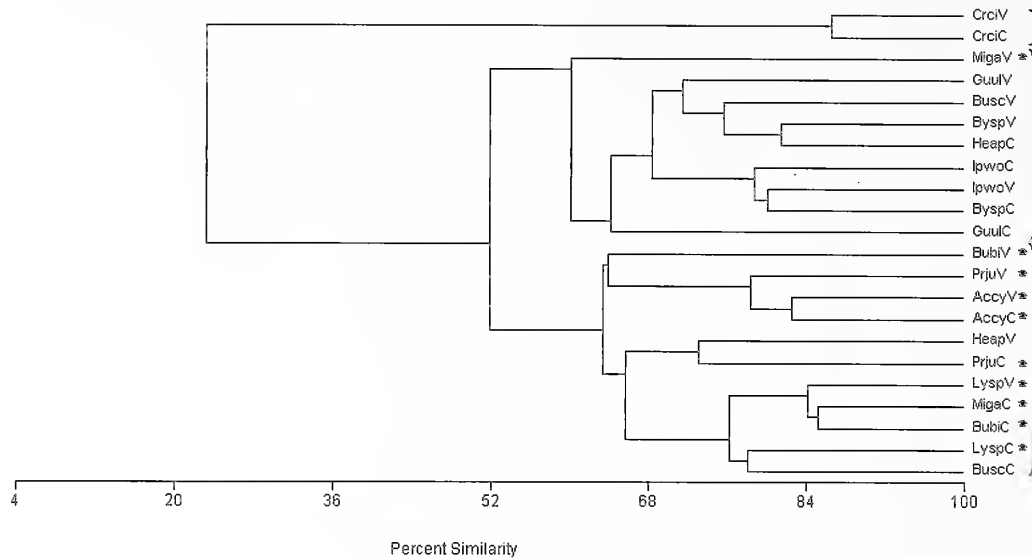


Figure 1.—Classification of 11 plant species in two sites according to spider species abundance. Plant codes are the same as in Table 1. The additional last capital letter represents the sample site (C = Caracol, V = Charco Verde). * = small-leaved species.

(30,240 and 16,301, respectively), while the broad leaved trees, *H. appendiculatus* and *I. wolcottiana*, had the lowest number of leaves (15 and 12.2, respectively) (Table 1). Mean number of branchlets per terminal branch was higher for *B. schlehtendalii* (22.5), *Bursera bipinnata* (22), and *G. ulmifolia* (21.5), while *C. ciliatoglanduliferus* (9) and *H. appendiculatus* (8) had the lowest values (Table 1). Mean plant height among species varied from 1.1 m (*C. ciliatoglanduliferus*) to 5.3 m (*H. appendiculatus*) (Table 1).

The dominant species in both sites was *A. cymbispina*, a shrub that grows in areas that have been altered by cattle and goat grazing. In both sites, *P. juliflora* was the second most abundant species. *C. ciliatoglanduliferus* is an invasive shrub particularly common in one site (El Caracol). In this site *M. galeottii* was also dominant, while *L. acapulcense* was common in Charco Verde (Table 2).

Spider abundance and composition.—A total of 1340 adult spiders belonging to 21 species were caught in the two sampled sites (667 in El Caracol, and 673 in Charco Verde) (Table 2). Species composition was similar in both sites. *Isaloides cf. yolotli* (Jiménez, 1992), *Hamataliwa puta* (O. Pickard-Cambridge 1894) and *Peucea viridans* (Hentz 1832) represented 73% of the total numbers caught in El Caracol and 69% in Charco Verde. Four species were represented by only one individual: *Micrathena gracilis* (Walckenaer 1805) and *Mallos* sp. in El Caracol, and *Euryopsis californica* Banks 1904 and *Ocrepeira* sp. in Charco Verde. The other species found were *Neoscona oaxacensis* (Keyserling 1864), *Euriophora edax* (Blackwall 1863), *Wamba crispulum* (Simon 1895), *Theridion* sp., *Mimetes puritans* Chamberlin 1923, *Tmarus ehecaltoatl* Jimenez 1992, *Misumenoides* sp., *Modysticus cf. floridana* (Banks 1895), *Apollophanes punctipes* (O.P.-Cambridge 1891), *Philodromus albicans* O. Pickard-Cambridge 1897, *Oxyopes bifidus* F.O. Pickard-Cambridge 1902, *Phidippus* sp., *Paramarpissa piratica* (Peckham & Peckham 1888) and *Metaphidippus cf. apicalis* F.O. Pickard-Cambridge 1901.

In both study sites, the dominant families were hunters, in particular Oxyopidae with 49% and 43% (El Caracol and

Charco Verde, respectively), followed by Thomisidae (36% and 38%). The family Salticidae was represented by 10% and 11% of the total catch. In spite of spiders being sampled from the foliage, web weavers were only represented by 1.5% of the total catch in El Caracol, and 5.1% in Charco Verde.

Spider species distribution.—A classification of the plants based on the spider abundances resulted in three main clusters at the 50% similarity level (Fig. 1). The first cluster separated *C. ciliatoglanduliferus* (Crci) from all other plant species. The second cluster included all the broad-leaved species with the exception of *M. galeottii* (MigaV) from Charco Verde, while the third cluster included all the small-leaved plants and two broad-leaved trees, *H. appendiculatus* (HeapV) from Charco Verde and *Bursera schlehtendalii* (BuscC) from El Caracol. The first division was explained by the presence of *P. viridans*, one of the most abundant species, which was found almost exclusively on *C. ciliatoglanduliferus*. Most spiders had higher abundances in small-leaved plants (Table 2), which explains the separation between the second and third clusters (Fig. 1).

The first two PCA axes based on spider abundances accounted for 88% of the variance (58% and 30%, respectively). Since some spider species had less than 5 individuals, only 15 out of 21 species were included in the analysis. Nine of these species were common to both sites. The first axis of the ordination (eigenvalue = 0.58) was negatively correlated with plant height ($r = -0.87$, $P < 0.001$). The ordination along this axis was determined by the large numbers of *P. viridans* on *C. ciliatoglanduliferus* (both had the highest scores on the positive side (Fig. 2). The second axis (eigenvalue = 0.55) was negatively correlated with foliage area ($r = -0.91$, $P < 0.001$) and positively with number of leaves ($r = 0.86$, $P < 0.001$) and branchlets ($r = 0.61$, $P < 0.05$). The ordination pattern along this axis clearly segregated all spider species and small-leaved bipinnate plants from broad-leaved plant species (Fig. 2). Spider species, as well as all small-leaved bipinnate species had positive scores. These plants had a high numbers of leaves and branchlets, and low foliage area (Table 1,

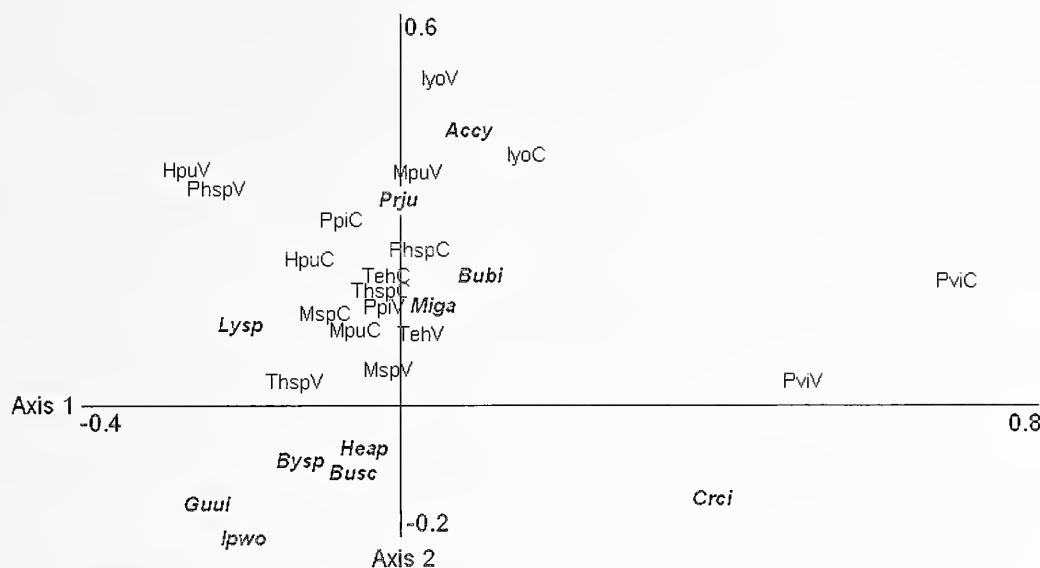


Figure 2.—Principal Components Analysis of the spider species present in 11 dry forest plant species. Spiders are: Pvi = *Peucetia viridans*, Iyo = *Isaloides cf. yollotl*, Hpu = *Hamataliwa puta*, Mpu = *Mimetes puritans*, Phsp = *Phidippus* sp., Ppi = *Paramarpissa piratica*, The = *Tmarus ehecacatl*, Thsp = *Theridon* sp., Misp = *Misumenoides* sp. In the codes for spider species names, the additional last capital letter represents the sample site (C = Caracol, V = Charco Verde). Codes for plant names are in bold and are the same as in Table 1.

Fig. 2). Conversely, the plant species on the negative side included those with high foliage area but low number of leaves and branchlets (Table 1, Fig. 2). The ordination shows the relationship of each spider species with the plants. For instance, *I. cf. yollotl*, a common spider species was particularly abundant on *A. cymbispina* and that is why these species appear together in Fig. 2.

DISCUSSION

In spite of intensive sampling (a total of 1540 branches during a seven month period), only 21 species were found among 1340 individuals collected in the two sampled sites (677 in El Caracol, and 673 in Charco Verde). Rarefaction analyses (P. Corcuera, unpublished results) showed that only two or three additional foliage species are likely to be found in the study area.

Small-leaved plants appear to be suitable sites for foliage spiders. Evans (1997) found that social crab spiders preferred *Eucalyptus* species with smaller leaves. Perhaps more importantly, and regardless of plant taxon, density of leaves per branch (e.g., Gunnarsson 1990; Souza & Martins 2005) as well as structural complexity are better predictors of spider diversity. Branching or twig density, as well as leaf density have been found to be strongly related with number of spiders, diversity, and abundance of various functional groups (Hatley & MacMahon 1980; Halaj et al. 1998; Corcuera et al. 2004). These variables also explained the spider distribution in this study.

A classification of the plant species (Fig. 1) separated most small-leaved bipinnate trees and shrubs from most broad-leaved species. The second axis of an ordination also segregated the plants and gave high positive scores to all spiders and small-leaved plants and negative to all broad-leaved (Fig. 2). This axis was positively correlated with number of leaves and branchlets and negatively with foliage area. The first axis was correlated with plant height and was explained by high numbers of *Peucetia viridans*, a very

common spider in the study sites and the only one that was associated with the small shrub *Croton ciliatoglanduliferus*.

Causal explanations for habitat preferences of foliage spiders have not been explored in depth but some hypothesis have been suggested. For example, *Peucetia* species are known to favor plants with glandular trichomes, presumably because arthropods are trapped by these hairs and represent available prey for the spider (Vasconcelos-Neto et al. 2006). Halaj et al. (1998) suggested that plants with higher cover are easier to locate and might provide more resources. This might explain higher diversities of most spiders on the most common trees and shrubs. Total number of individuals was significantly correlated with plant cover in the two sites ($r = 0.83$, $P < 0.005$ for El Caracol and $r = 0.67$, $P < 0.05$ for Charco Verde). This may explain why *A. cymbispina*, which had the highest plant species cover in both sites, supported high densities of most spiders (Table 2). In the same way, *M. galeotti*, a small-leaved tree from Chaco Verde, was included in the broad-leaved cluster in the classification (Fig. 1, Table 2). This species had low densities of spiders probably because of its low cover in this site. However, *P. juliflora* and *B. bipinnata*, with high richness and species abundances, had very small cover in one or both sites (Table 2). Plants with higher cover might be easier to locate, but they do not necessarily provide more resources. Other factors (i.e., branch and leaf density) appear to be more important to understand the distribution of foliage spiders.

Some plant attributes might provide suitable microclimatic conditions. Riechert & Tracy (1975) suggested that certain plants might be favored because of their ability to modify the thermal environment. In hot climates with long drought periods, preserving body temperature would be a most important factor. Small-leaved plants, especially *C. cymbispina* and *P. juliflora* could provide a cooler environment because they either do not shed their leaves (as does *P. juliflora*) or remain green during the early draught, which is when

spiderlings start to disperse. This species also starts producing leaves early, before the rains, when broad-leaved trees and shrubs are still deciduous. Once settled on these plants, there would be no reason to move to shrubs or trees where conditions would be less favorable.

Besides resource availability and favorable physical conditions, accessibility of refuges against predators plays an important role in determining spider distribution. Gunnarsson (1996) suggested that high leaf densities could provide shelter from bird predation. This would not seem the case in our study sites, since bird attacks tended to be more frequent in small-leaved trees and shrubs (Corcuera 2001), where spiders are more abundant.

Few studies have compared differences in the abundance of spiders on foliage of different shrub and tree species (e.g., Halaj et al. 1998; Raizer & Amaral 2001; Souza & Martins 2004). Although some spider species were found in small numbers (< 5 individuals), and it is not possible to reach any conclusions about their distribution, our results reveal that foliage spider species were positively influenced by small-leaved trees and shrubs with a high number of leaves and branches, and negatively by broad-leaved plants with a high foliage area among 11 plant species of the Mexican tropical dry forest.

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Microhabitat preferences for the errant scorpion, *Centruroides vittatus* (Scorpiones, Buthidae)

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Abstract. Vegetation as a preferred microhabitat for scorpions has rarely been considered despite many Buthidae (the bark scorpions) being non-burrowing errant scorpions that are active on both the ground and vegetation. Microhabitats can serve multiple functions for *Centruroides vittatus* (Say 1821), but a particular microhabitat can be preferred for a certain function such as a refuge, foraging, or feeding.

Observations of microhabitat use by *C. vittatus* were performed in Laredo, Texas of the Tamaulipan Biotic Province. Comparisons of microhabitat use by *C. vittatus* at different temperatures or precipitation levels were performed. Foraging and feeding by *C. vittatus* among microhabitat classes were also compared. The observed use of vegetation by *C. vittatus* during different seasons was compared to the expected use based on relative abundance of vegetation in the habitat.

Air temperature, but not precipitation, had a significant effect on microhabitat use by *C. vittatus*. Microhabitat had a significant effect on foraging of *C. vittatus* with caterpillars comprising 34.6% of the prey items and half of the scorpions feeding on caterpillars were in blackbrush (*Acacia rigidula*). The lowest proportion of scorpions observed feeding was on the ground (3.8%) and the highest in blackbrush (40.4%). The frequency of *C. vittatus* among vegetation classes was significantly different compared to the relative abundance of plant species in the plot. Scorpions were observed on prickly pear cactus (*Opuntia engelmannii*) and strawberry cactus (*Echinocereus emeacanthus*) at a higher frequency than expected, and scorpions were observed on guajillo (*Acacia berlandieri*) and tasajillo (*Opuntia leptocaulis*) at a lower frequency than expected. The frequency of scorpions on blackbrush was higher than expected during the spring.

Vegetation is an important microhabitat for *C. vittatus* in south Texas. The results indicate the possibility that *C. vittatus* in south Texas used various plant species to carry prey captured on the ground into vegetation to feed, used blackbrush to forage for caterpillars, and used strawberry and prickly pear cacti as a possible refuge.

Keywords: Habitat selection, foraging, refuge, feeding

Scorpions utilize a diversity of habitats (Hadley & Williams 1968; Polis 1990). Studies of habitat selection by scorpions have compared soil types for foraging (Polis & McCormick 1986a) or to build burrows (Polis & Farley 1980; Bradley & Brody 1984; Bradley 1988; Smith 1998). The effects of vegetation on scorpions has been considered in association with soil types (Bradley 1988), fire (Smith & Morton 1990), or as refuge from predation or cannibalism (Polis 1980a) including scorpions fleeing under vegetation to avoid predators because of low light levels (Camp & Gaffin 1999). However, vegetation as a preferred microhabitat for scorpions has rarely been considered despite many Buthidae (the bark scorpions) being non-burrowing errant scorpions that are active on both the ground and vegetation (Hadley & Williams 1968; Polis 1990).

Centruroides vittatus (Say 1821) (Scorpiones; Buthidae), the striped bark scorpion, has a wide distribution utilizing a number of different habitats (Shelley & Sissom 1995). Studies of habitat use by *C. vittatus* have already been done in the desert of west Texas (Brown & O'Connell 2000; Brown et al. 2002), in the deciduous forest of Arkansas (Yamashita 2004), and in the chaparral of south Texas (McReynolds 2004). This study will consider if *C. vittatus* has microhabitat preferences that can increase the fitness of the scorpion in the chaparral of south Texas.

Centruroides vittatus can utilize microhabitats for a refuge, foraging, or feeding. Many buthids will use vegetation or debris as a refuge during the day (Polis 1990). Refuges such as burrows can be used to avoid extreme temperatures during the day for many species of scorpions (Hadley 1974), and rocks

and cracks in the ground can serve the same function for *Centruroides sculpturatus* Ewing 1928 (Crawford & Krehoff 1975) and *C. vittatus* (Brown et al. 2002). Vegetation could also be a refuge from extreme conditions such as high temperatures during the day or low temperatures at night. One possibility is that cacti such as Texas prickly pear cactus (*Opuntia engelmannii*), tasajillo (*Opuntia leptocaulis*) and strawberry cactus (*Echinocereus emeacanthus*) can be a refuge from these extreme conditions because the high water content in the cacti could provide a buffer from temperature changes due to the high specific heat of water.

Centruroides vittatus can climb into vegetation to forage or to feed on prey captured on the ground. Brown & O'Connell (2000) hypothesized that *C. vittatus* climbs into vegetation because of predator avoidance or higher prey availability. If feeding scorpions carry prey up vegetation to avoid ground predators (such as Lycosidae and Solifugae), then any vegetation can be used as a site to feed assuming that all plant species provides the same protection from ground predators. In addition, feeding scorpions carrying prey up vegetation from the ground should mainly feed on prey that is captured on the ground (Brown & O'Connell 2000). If scorpions are foraging in vegetation, then scorpions can be searching for prey found only in vegetation (e.g., lepidopteran caterpillars) and should prefer vegetation with high availability of these prey such as blackbrush (*Acacia rigidula*) and guajillo (*Acacia berlandieri*). Furthermore, scorpions can forage in the vegetation when prey availability in vegetation is higher such as during periods of high precipitation (see Polis 1979, 1980b).

Microhabitats can serve multiple functions for *C. vittatus*, but a particular microhabitat can be preferred for a certain function. This study will consider how certain conditions can affect microhabitat use by scorpions. Microhabitat use will be compared in relation to temperature and precipitation for possible shifts in activity among microhabitats. Microhabitat use will be compared in relation to prey capture and feeding to determine if scorpions are foraging in vegetation and/or carrying prey from the ground to vegetation. The observed use of trees, shrubs and cacti by *C. vittatus* during three time periods will be compared to a census of plant species. These comparisons are to determine if microhabitat selection was random or *C. vittatus* shows a preference for microhabitats during any seasonal periods.

METHODS

Study animal.—*Centruroides vittatus* has a wide distribution with Laredo, Texas in the southern portion of the distribution (Shelley & Sissom 1995). *Centruroides vittatus* is nocturnal with refuges during the day in debris, beneath vegetation, under bark, and in holes in the ground, but *C. vittatus* and other bark scorpions rarely dig their own burrows (Polis 1990). Scorpions emerge from their refuge only occasionally to forage (Polis 1980b; Bradley 1988; Warburg & Polis 1990). Different sized scorpions can be observed throughout the year with birth of *C. vittatus* between April and September and age of maturity of 36 to 48 mo (Polis & Sissom 1990). On nights of emergence, *C. vittatus* is active on the ground and/or in vegetation. Courtship by *C. vittatus* has rarely been observed and females carrying first instars observed only occasionally in the field (pers. obs.). Voucher specimens of *C. vittatus* were deposited in the invertebrate collection at Texas A&M International University.

Habitat.—This study was done on the campus of Texas A&M International University (27°35'N, 99°26'W), Laredo, Texas. Laredo is in the Tamaulipan Biotic Province that is characterized by low precipitation and high average temperatures (Blair 1950). The habitat of the research plots can be described as thorny brush (Blair 1950) or chaparral. Vegetation in the plots included blackbrush (*Acacia rigidula*), guajillo (*Acacia berlandieri*), honey mesquite (*Prosopis glandulosa*), Texas prickly pear cactus (*Opuntia engelmannii*), tasajillo (*Opuntia leptocaulis*), strawberry cactus (*Echinocereus enneacanthus*), cenizo (*Leucophyllum frutescens*), guayacan (*Guaia-cum angustifolium*), leather stem (*Jatropha dioica*), lotebush (*Ziziphus obtusifolia*), Spanish dagger (*Yucca treculeana*), and other species. Three research plots of the campus were studied from 14 September 2000 to 8 August 2002 over 20 nights in 2000, 67 in 2001, 15 in 2002. The study continued from 28 August 2002 to 12 May 2005 in the main research plot over 21 nights in 2002, 52 in 2003, 46 in 2004, and 26 in 2005. At the start, three circular sites of 100 m² were placed in each plot to include different vegetation. Additional sites were placed at random in the main research plot, and these sites were first searched on 1 November 2000. The sites in the other two plots were abandoned 8 August 2002 because of construction nearby and light pollution from streetlights on the campus.

Data collection.—Scorpions were observed at night by locating the scorpion fluorescing under ultraviolet light (see Sissom et al. 1990). Observed scorpions were active and either

out of or just emerging from their refuges. No data were collected on scorpions in their refuges to avoid destruction of the habitat. Scorpion data were collected after sunset between 19:30 Central Standard Time, USA (CST) at the earliest and 01:00 CST at the latest for an average of two hours per night of observation. Sites were selected at random and searched during a night of observation with a mode of three sites searched per night. Data were collected on all scorpions observed within or near the site. Data collected for each scorpion included date and time of observation, species of scorpion, microhabitat used, if prey was captured or not, and prey taxa. Air temperature was collected each night using a portable weather meter, Kestrel® 3000, from 16 July 2000 to 12 May 2005. Precipitation data were radar estimates for the field site that were provided by the Center for Earth and Environmental Studies, Texas A&M International University from 1 June 2003. Total precipitation for the two weeks just prior to the sample night was used for analysis because precipitation for the prior two weeks showed a significant effect on the prey availability in blackbrush (unpubl. data). All months of a year were sampled, but scorpions were rarely active during December and January. Scorpions can be active during all other months especially when the temperature is above 20° C during the night. Data collection occurred during 94 nights between January–April, 66 nights between May–August, and 115 nights between September–December.

The microhabitat data were placed in different classes: ground, grass, blackbrush, guajillo, prickly pear cactus, tasajillo, strawberry cactus, and other vegetation for the comparisons in this paper. If observed on soil, leaf litter, or a rock, the scorpion was considered on the ground. Grasses were not identified to species, but all other plants were identified to species if possible. Other vegetation included small trees that are rarely taller than 2 meters with the exception of a few mesquites and perennial shrubs such as cenizo, guayacan, leather stem, lotebush, and Spanish dagger. Mesquite was included in other legumes instead of other vegetation for the comparison of prey captured in different microhabitats. Annuals were rare in the habitat except for ephemeral wildflowers after heavy rains and scorpions were rarely observed climbing these wildflowers. Prey capture classes included no prey captured, caterpillars (Lepidoptera larvae), other insects (including adult Lepidoptera), and IGP (intraguild prey including Scorpiones, Araneae, Solifugae, and Chilopoda). Prey capture by scorpions can be observed as scorpions digest externally, thus prey items can be observed in pedipalps or chelicerae (Polis 1979).

Census of vegetation.—A census of plant species in the main research plot was performed on four randomly selected sites from the 12 sites in use during the summer of 2001 and the spring of 2002. Each circular site had all trees, shrubs and cacti within the 100 m² area identified to species and counted (Table 1). Grasses and ephemeral wildflowers were not sampled. The proportions of plant species in the four sites can be used to predict the expected frequency of scorpions on vegetation as if there was no preference in vegetation use (Table 1). Only scorpions on live vegetation that were included in the census were included in the comparisons (no scorpions on the ground, grass, ephemeral wildflowers, or dead vegetation). The observed vegetation use of *C. vittatus* in

Table 1.—The number, proportion (%), and estimated density of plant species censused from four random sites in the main research area during the summer of 2001 and spring of 2002. Each site was a circle with an area of 100 m².

Species	Common name	Number	Proportion (%)	Density (#/ha)
<i>Acacia rigidula</i>	Blackbrush	51	28.3	1275
<i>Acacia berlandieri</i>	Guajillo	33	18.3	825
<i>Opuntia leptocaulis</i>	Tasajillo	33	18.3	825
<i>Opuntia engelmannii</i>	Prickly pear cactus	12	6.7	300
<i>Guaiacum angustifolium</i>	Guayacan	12	6.7	300
<i>Echinocereus enneacanthus</i>	Strawberry cactus	5	2.8	125
<i>Jatropha dioica</i>	Leather stem	5	2.8	125
<i>Prosopis glandulosa</i>	Honey mesquite	2	1.1	50
	Other vegetation	27	15.0	675
	Total	180		4500

the main research plot during three time periods was compared to the expected vegetation use. The three time periods were based on a previous analysis of seasonal differences in microhabitat use (McReynolds 2004).

Data analyses.—Analysis of contingency tables (Model I) for effects on microhabitat and foraging used the G-test of independence (Sokal & Rohlf 1995). Planned comparisons were performed on a significant association for the contingency tables to test predictions on microhabitat preferences. The first planned comparison was among ground and vegetation. The second planned comparison was either to test for differences among vegetation classes that were predicted to be used for foraging (*Acacia* spp.), for refuges (cacti) and other vegetation or to test for differences in prey capture among legumes (*Acacia* spp. and *Prosopis glandulosa*) and other vegetation. Other comparisons were performed to complete the orthogonal comparisons. The replicated goodness of fit G-test was used to compare the observed vegetation use by *C. vittatus* for three time periods to the expected vegetation use based on the census of vegetation (Sokal & Rohlf 1995).

RESULTS

Effects on microhabitat use.—Air temperature had a significant effect on microhabitat use (Fig. 1). In planned comparisons, ground classes were significantly different from pooled vegetation classes, blackbrush classes were significantly different from guajillo classes, and grass classes were marginally significantly different from other vegetation classes (Fig. 1, Table 2). However, there was no significant difference among *Acacia* spp., cacti, or other vegetation classes (Fig. 1, Table 2). The proportion of scorpions on vegetation was highest at intermediate temperature class (20–25° C) and lowest at high temperature class (> 30° C) (Fig. 1). Precipitation for the two weeks prior to observations had no significant effect on microhabitat use (Fig. 2).

Foraging.—Microhabitat had a significant effect on foraging of *C. vittatus* (Fig. 3). In planned comparisons, ground was significantly different from all vegetation, and legumes were significantly different from other vegetation (Fig. 3, Table 3). Only a very small proportion of scorpions on the ground had prey compared to scorpions in vegetation. The scorpions in the legumes had a high proportion of caterpillars and other insects as prey while the scorpions in other vegetation and cacti had a high proportion of intraguild prey (IGP). The lowest proportion of scorpions observed feeding (n

= 104) was on the ground (3.8%) and the highest in blackbrush (40.4%). Caterpillars were 34.6% of the prey items for *C. vittatus*, and half of the scorpions observed feeding on caterpillars were in blackbrush. Intraguild prey (IGP) were 17.3% of the prey items for *C. vittatus* with 9.6% Araneae, 3.8% Scorpiones, 1.9% Solifugae, and 1.9% Chilopoda.

Microhabitat preferences.—The proportion of *C. vittatus* on vegetation was compared to the expected proportion for three time periods (Fig. 4). The expected proportion assumed that scorpions have no preference for vegetation, and the distribution of scorpions on vegetation will be random relative to the abundance of plant species in the research plot (see Table 1). The proportion of scorpions on vegetation was significantly different from expected for all three time periods and the pooled data, and the three time periods were significantly heterogeneous (Fig. 4, Table 4). Scorpions were observed on prickly pear and strawberry cacti at a higher frequency than expected for every time period and the pooled data, and scorpions were observed on both guajillo and tasajillo at a lower frequency than expected for every time period and the pooled data. However, the frequency of scorpions on blackbrush was higher than expected during the January–April time period but lower than expected during the May–August time period and only slightly higher than expected during the September–November time class. The heterogeneity between time periods was due to fluctuations in the frequency of scorpions in the blackbrush and other vegetation classes.

DISCUSSION

Comparisons of scorpions have often noted the lack of activity on vegetation (Bradley 1988; Warburg & Polis 1990). One explanation for this pattern is that adaptation to a specialized habitat (sand) can reduce effectiveness in climbing (see Fet et al. 1998). However, bark scorpions (Buthidae) are known to be active on vegetation (Polis 1990). Microhabitat use of *Buthus occitanus* (Amoreux 1789) includes juveniles on bushes but not adults (Skutelsky 1996). In a study by Hadley & Williams (1968), *Centruroides sculpturatus* pursues prey up and down vegetation and under rocks and is more active than the other scorpion species. *Centruroides vittatus* in south Texas (present study) uses vegetation at higher frequency than in west Texas (Brown & O'Connell 2000) and in Arkansas (Yamashita 2004). Vegetation is important microhabitat for *C. vittatus* in Laredo, Texas with 54.1% on trees, shrubs or

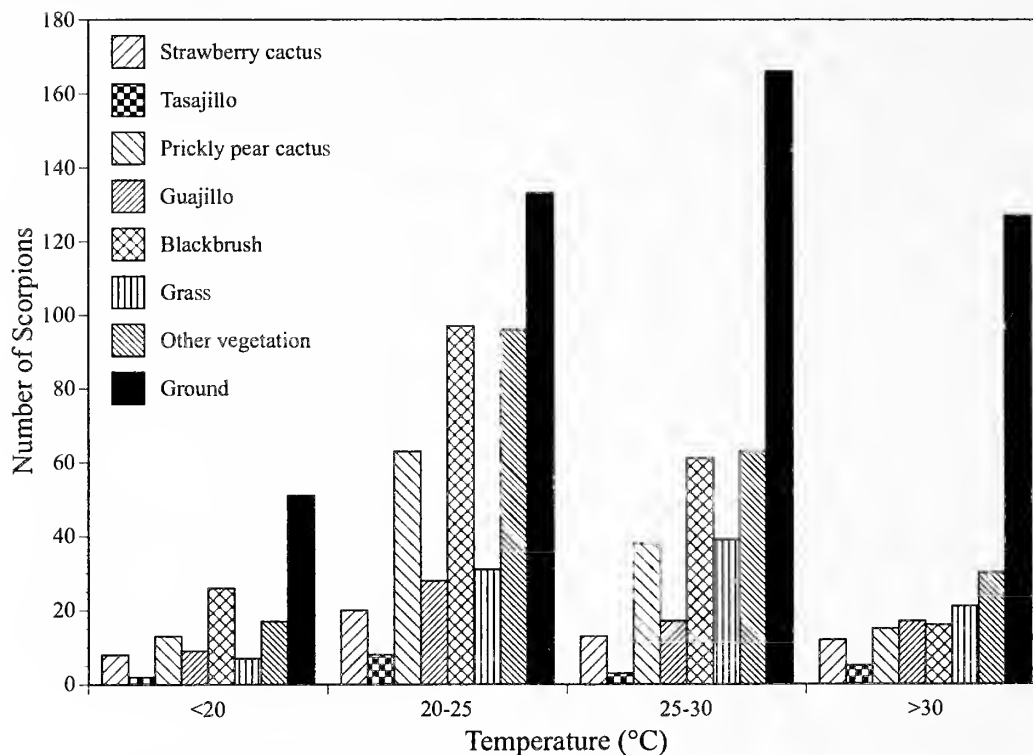


Figure 1.—The number of *Centruroides vittatus* using different microhabitats among temperature classes. The two *Opuntia* spp. classes, *O. leptocaulis* (tasajillo) and *O. engelmannii* (prickly pear cactus), were pooled for the statistical analysis. The frequency of microhabitat use was significantly different among temperature classes ($G = 74.79$, $P < 0.001$, $df = 18$, $n = 1252$). See Table 2 for planned comparisons among microhabitat classes.

cacti; 7.8% on grass and only 38.1% on the ground. In other studies, *C. vittatus* were observed in trees (9.1%) and grass (10.6%) in Arkansas (Yamashita 2004) and 26.4% climbing vegetation in west Texas (Brown & O'Connell 2000).

Scorpion activity and thus microhabitat use can shift because of environmental factors (i.e., temperature and/or precipitation). The environmental factors can have a direct effect on the scorpion activity or indirectly on prey availability (Polis 1980a, 1988 but see Bradley 1988). Microhabitat use of *C. vittatus* shifted to the ground at high nocturnal temperatures. However, there was no support for the prediction that microhabitat use would shift from refuges in cacti to foraging in *Acacia* spp. with differences in temperature although the use of blackbrush was high during intermediate temperatures relative to guajillo. The high activity of scorpions on the

ground at high temperatures ($> 30^{\circ}\text{C}$) during the night does fit the pattern of high activity of *C. vittatus* on the ground during July and August as previously reported (McReynolds 2004). This can indicate low prey availability in vegetation and relatively higher prey availability on the ground during the hottest period of the year. Microhabitat use of *C. vittatus* did not shift with precipitation, and there was no evidence that foraging in blackbrush increased with high precipitation as predicted because of the observed increase in caterpillar availability with high precipitation (unpubl. data). One possible reason that activity and foraging behavior does not change with precipitation (and prey availability) is the threat of predation including cannibalism by adults on juveniles (see Polis 1980a, 1980b). Only adult *Paruroctonus mesaensis* (now *Smeringus mesaensis* (Stahnke 1957)) have a significant positive correlation with prey availability while the other age classes have a positive but not significant correlation (Polis 1980b).

Table 2.—Planned comparisons among microhabitat classes of the contingency table for microhabitat vs. temperature classes. The two *Opuntia* spp. classes, *O. leptocaulis* (Tasajillo) and *O. engelmannii* (Prickly pear cactus), were pooled for the statistical analysis. NS = not significant. See Fig. 1.

Planned comparisons	<i>G</i>	<i>df</i>	<i>P</i>
Ground vs. All vegetation	43.71	3	< 0.001
Cactus vs. <i>Acacia</i> spp. vs. Grass and Other vegetation	8.71	6	NS
<i>Opuntia</i> spp. vs. Strawberry cactus	3.77	3	NS
Blackbrush vs. Guajillo	11.33	3	< 0.05
Grass vs. Other vegetation	7.27	3	0.1–0.05
Total	74.79	18	< 0.001

Scorpions can utilize different microhabitats and in particular different vegetation for feeding, foraging or refuge. Scorpion species can feed where the prey was captured, can carry prey to burrow (or other refuge) before feeding, or can carry it into vegetation. For example, *Parabuthus pallidus* Pocock 1895 carries prey back to the burrow but *Parabuthus leiosoma* (Ehrenberg 1828) feeds where prey is captured (Rein 2003). Scorpions with prey on vegetation are usually attributed to scorpions carrying prey from the ground into vegetation to feed (Polis 1979; Brown & O'Connell 2000). Only 3.8% of the scorpions with prey were on the ground in south Texas but many prey of *C. vittatus* were usually

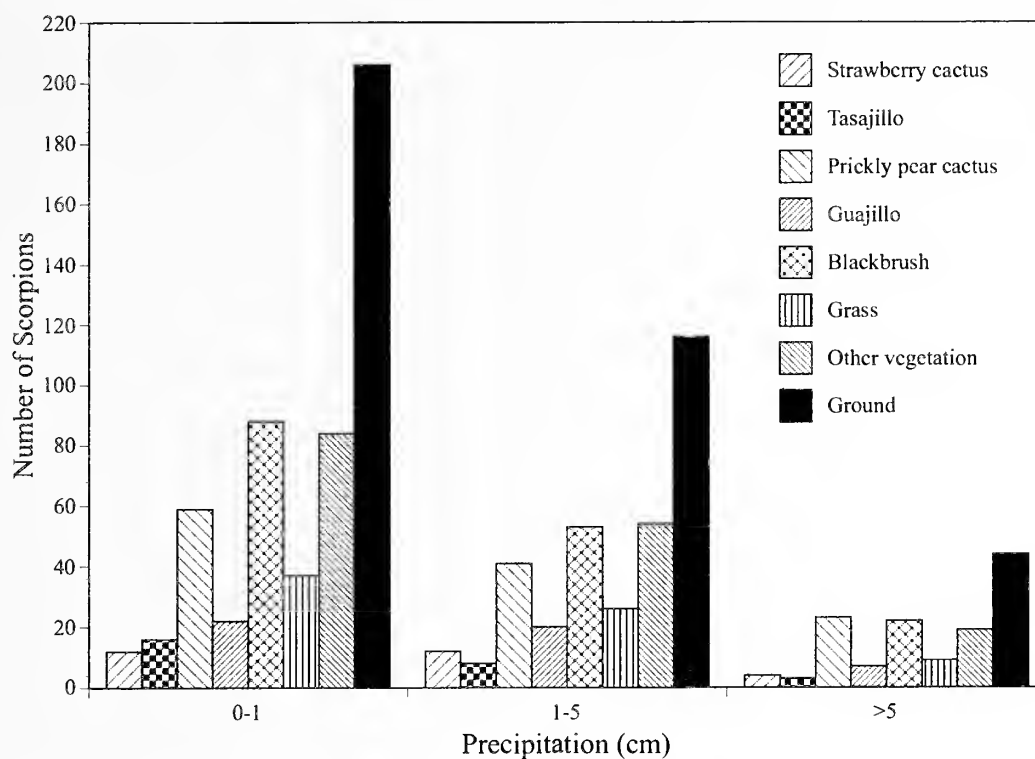


Figure 2.—The number of *Centruroides vittatus* using different microhabitats among classes of total precipitation for the prior two weeks. The frequency of microhabitat use was not significantly different among precipitation classes ($G = 7.37$, not significant, $df = 14$, $n = 985$).

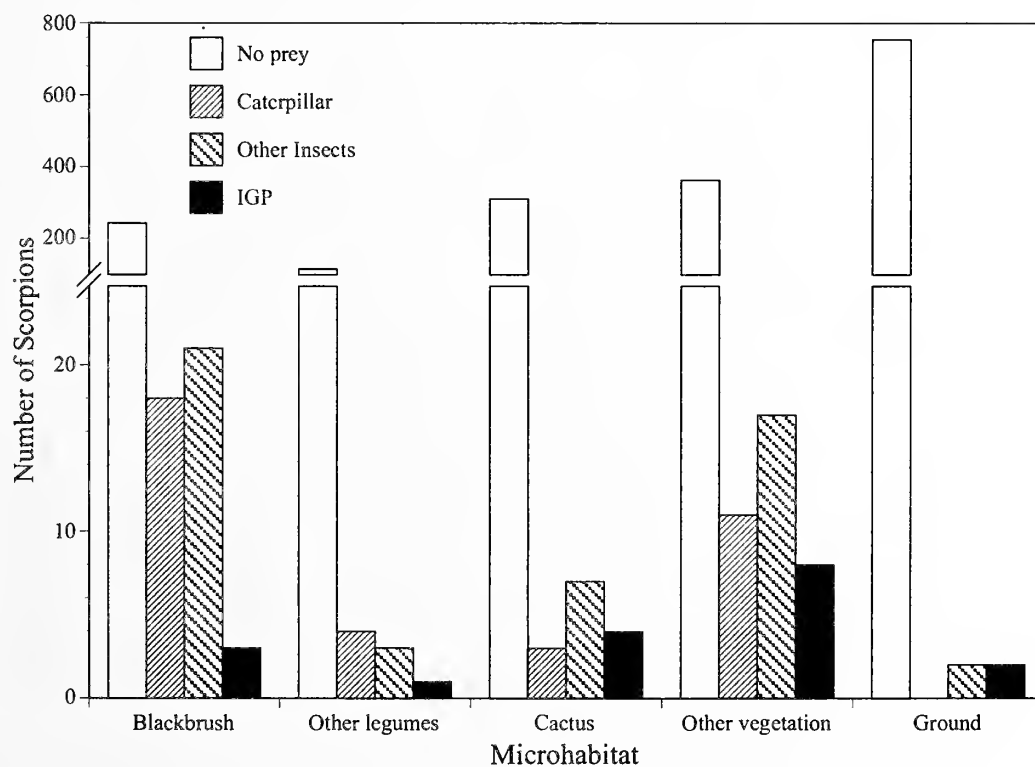


Figure 3.—The number of *Centruroides vittatus* using different microhabitats among prey capture classes. The frequency of microhabitat use was significantly different among prey capture classes ($G = 112.17$, $P < 0.001$, $df = 12$, $n = 1890$). See Table 3 for planned comparisons among microhabitat classes.

Table 3.—Planned comparisons among microhabitat classes of the contingency table for microhabitat vs. prey capture classes. NS = not significant. See Fig. 3.

Planned comparisons	G	df	P
Ground vs. All vegetation	83.77	3	< 0.001
Legumes vs. Cactus and Other vegetation	14.92	3	< 0.01
Blackbrush vs. Other legumes	6.53	3	NS
Cactus vs. Other vegetation	6.95	3	NS
Total	112.17	12	< 0.001

observed on the ground (e.g., many of the intraguild prey) (pers. obs.). Intraguild prey (including cannibalism) were 17.3% of the prey in south Texas as compared to 27.91% of spider prey and 9.30% cannibalism for *C. vittatus* in Arkansas (Yamashita 2004). These data indicate that *C. vittatus* in south Texas do carry prey captured on the ground into vegetation to feed. One possible function of moving prey (including intraguild prey) to vegetation is to avoid intraguild predation (see Bradley & Brody 1984; Polis & McCormick 1986b, 1987). Another possible function can be to avoid scavenging ants. Ants were observed causing feeding scorpions to move (pers. obs. by E. Lopez and C.N. McReynolds). Scorpions can also move between vegetation. A scorpion was observed feeding on a caterpillar on tasajillo but near a blackbrush where the caterpillars are available (pers. obs.). Perhaps this is to avoid ants or predators (e.g., other scorpions).

Foraging in vegetation has not been considered important for scorpions (Polis 1979) except for errant scorpions (McCormick & Polis 1990) and by juveniles (e.g., juvenile *Buthus occitanus* ambush prey in vegetation but not adults (Skutelsky 1996)). There was no evidence of foraging in vegetation by *C. vittatus* in west Texas (Brown & O'Connell 2000). However, the diet of *C. vittatus* in Laredo, Texas includes a number of items that have a high availability in trees or shrubs. Caterpillars were an important prey item for the scorpions in south Texas and most of the caterpillar taxa captured by *C. vittatus* were available in blackbrush (unpubl. data). Caterpillars are rarely reported as an important item in the diet for scorpions (see McCormick & Polis 1990). Caterpillars were only 1.4% of the diet for *P. mesaensis* (Polis 1979), and no caterpillars were reported for *C. vittatus* in west Texas (Brown & O'Connell 2000) but 11.6% of the prey for *C. vittatus* in Arkansas (Yamashita 2004) and 34.6% in south Texas (present study). It is predicted that scorpions foraging in blackbrush (and other legumes) will increase when caterpillar availability increases. However, scorpions prefer blackbrush only in January–April and there is no shift to blackbrush with high precipitation. If caterpillar availability is higher with the blooming of blackbrush in March and April, then this can explain why there is not an overall preference for blackbrush but there is a higher proportion of prey captured during March and April (McReynolds 2004) and the proportion of scorpions on blackbrush is higher than expected during the January–April time period.

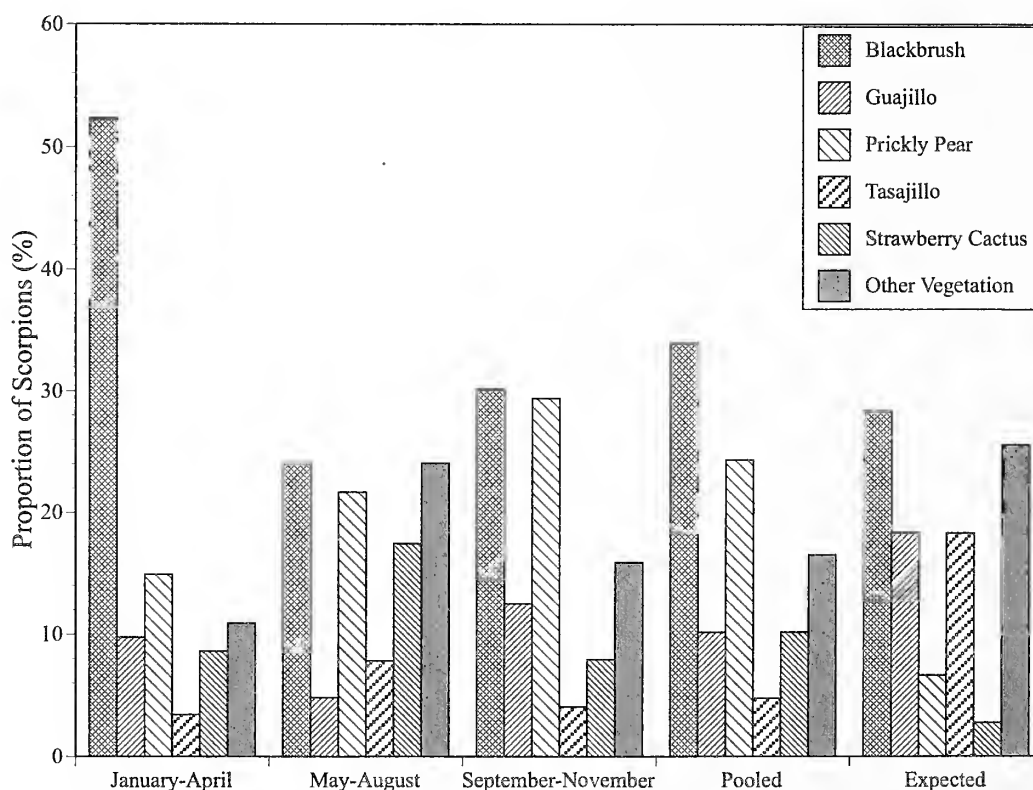


Figure 4.—The proportion (%) of *Centruroides vittatus* on vegetation during each seasonal time period compared to the expected proportion (%) on vegetation. The observed frequency of scorpions on vegetation from January to April ($n = 174$), from May to August ($n = 166$), from September to November ($n = 415$) and for the pooled data ($n = 755$) were compared to the expected frequency based on relative abundance of vegetation (see Table 1) in the replicated goodness of fit test (see Table 4).

Table 4.—Replicated goodness of fit test for microhabitat classes comparing the observed frequency of scorpions on vegetation to the expected frequency based on relative abundance of vegetation (see Table 1) during three seasonal time periods. See Fig. 4.

Time Periods	G	df	P
January to April	113.74	5	< 0.001
May to August	130.43	5	< 0.001
September to November	293.61	5	< 0.001
Pooled	473.47	5	< 0.001
Heterogeneity	64.31	10	< 0.001
Total	537.77	15	< 0.001

Most scorpion species dig a burrow, but many buthids do not dig their own burrow but use holes, space beneath rocks, and openings under bark and below vegetation as diurnal refuges (Polis 1990). *Centruroides vittatus* in west Texas have patchy distribution under rocks as diurnal refuges (Brown et al. 2002). Scorpions have been observed entering cracks or holes in the ground in south Texas (pers. obs.), but rocks are not available in the main research plot of this study. An alternative refuge for *C. vittatus* in south Texas can be a cactus because the high water content can provide a buffer from temperature changes due to the high specific heat of water. Scorpions have been observed going under the pads of a prickly pear cactus or down the openings between the stems of a strawberry cactus (pers. obs.). This can explain the higher than expected frequency of *C. vittatus* on strawberry cactus and prickly pear cactus in the research plot despite the low frequency of scorpions feeding on cacti and the low probability of foraging success because of the low prey availability on cacti (pers. obs.). This is assuming that *C. vittatus* is a central place forager (Orians & Pearson 1979) and there is a high probability that the scorpion would be near its refuge after emerging for the night (see Polis et al. 1985). However, *C. vittatus* has a lower than expected frequency in tasajillo. Perhaps tasajillo with thin stems and the more treelike structure does not provide the refuge that the prickly pear cactus or the strawberry cactus can provide. Sampling of potential refuges during the day at different temperatures will be required to establish diurnal refuge preferences of *C. vittatus* in south Texas (see Brown et al. 2002).

The high frequency of scorpions with prey in vegetation and low frequency on the ground indicates that *C. vittatus* carry prey caught on the ground into vegetation to feed. Foraging by *C. vittatus* especially in blackbrush for caterpillars has been demonstrated. However, the prediction that foraging scorpions will show a preference for blackbrush and other legumes was not supported. The frequency of scorpions in blackbrush did not increase with higher precipitation as is predicted because high precipitation increases availability of caterpillars in blackbrush. The frequency of scorpions in blackbrush was higher than expected in comparison to relative abundance of plant species only in January through April. It is possible that prey availability is higher early in the year especially March and April, but there is no evidence yet supporting this prediction. The results show that *C. vittatus* in south Texas used strawberry and prickly pear cacti with a higher than expected frequency in all time periods. However, the low frequency of scorpions with prey on cacti suggests that this

preference for cacti was not for feeding or foraging, and perhaps scorpions were utilizing the cacti for another function such as a diurnal refuge.

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Observations on phenology and overwintering of spiders associated with apple and pear orchards in south-central Washington

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Abstract. Beating tray and sweep net samples from apple and pear orchards in south-central Washington State were used to obtain information on life history and phenology of orchard-associated spiders. Cardboard shelters placed in the orchards in the fall and collected during the winter yielded information on spider overwintering. Data were obtained for 43 species in 28 genera and 12 families. The eight most abundant species were *Pelegrina aeneola* (Curtis 1892), *Meioneta fillmorana* (Chamberlin 1919), *Oxyopes scalaris* Hentz 1845, *Theridion neomexicanum* Banks 1901, *Misumenops lepidus* (Thorell 1877), *Xysticus cunctator* Thorell 1877, *Philodromus cespitum* (Walckenaer 1802), and *Sassacus papenhoei* Peckham & Peckham 1895. Each was represented by more than 690 specimens. Salticidae, Philodromidae, and Linyphiidae were represented by the largest number of species. Most species appear to have univoltine life cycles in the study area. Species matured at different times during the season between spring and fall. Twenty-seven species utilized cardboard shelters for overwintering, but some common spiders failed to do so and apparently use alternative locations. Some species overwintered in a broad range of developmental stages, whereas other species overwintered in only one or two instars.

Keywords: Araneae, life history, seasonality

Spiders have been of interest as predators of arthropod pests in orchards for at least 50 years. Chant (1956) found differences between the spider faunas of insecticide treated compared to untreated orchards and listed the natural (i.e., non-orchard) habitats in which many species occurred. Dondale (1956, 1958) recorded 77 species from apple orchards in Nova Scotia, Canada, provided data on abundance, and observed spiders feeding on apple pests. Similar studies were conducted over the next 35 years: Dondale et al. (1979) and Bostanian et al. (1984) in Canada; Specht & Dondale (1960), Legner & Oatman (1964), and McCaffrey & Horsburgh (1980) in the United States; Mansour et al. (1980a) in Israel; Dondale (1966) in Australia; and Hukusima (1961) in Japan. The efficacy of limb tapping for estimating spider populations in apple orchards was investigated by McCaffrey et al. (1984).

Interest in the spider fauna of apple orchards has continued in recent years as pest management programs that rely less heavily on broad-spectrum insecticides are employed with greater frequency, improving the prospects for significant impact by natural enemies on pest control. Studies have examined the tree canopy fauna (Olszak et al. 1992; Wisniewska & Prokopy 1997; Brown et al. 2003; Pekar & Kocourek 2004), the soil surface fauna (Bogya & Marko 1999; Pekar 1999a; Epstein et al. 2000), and the fauna of the herbaceous layer (Pekar 1999b; Bogya et al. 2000; Miliczky et al. 2000). Overwintering spiders (Bogya et al. 2000; Pekar 1999c; Horton et al. 2001) and the bark dwelling fauna (Bogya et al. 1999b) have also received attention. Regional geographic effects were found to be most important in determining the composition of spider assemblages in orchards in different areas (Bogya et al. 1999a).

The phenologies of numerous spider taxa have been documented by field and laboratory studies (Merrett 1967, 1968; Aiken & Coyle 2000; Stiles & Coyle 2001). Annual, biennial, and intermediate length life cycles have been described (Toft 1976, 1978; Wise 1984), and in some cases a species' life cycle has been found to vary within its range,

probably influenced by local climatic conditions (Dondale 1961; Putman 1967). Schaefer (1977) distinguished five types of life cycle among spiders from a north temperate region, studied their adaptive strategies for surviving the winter, and noted the importance of the cold season in synchronizing a species' life cycle.

Here we report on spiders that are found in apple and pear orchards in Yakima County, Washington, an important fruit growing area of the state. Life cycles of several common, orchard-associated species are described, and seasonal distribution data for adults and penultimate stage males of less common species are presented. Information on species that utilized artificial shelters for overwintering is also given. Information of this kind may be useful in assessing the potential contribution of spiders to orchard pest control and in scheduling pesticide applications to minimize adverse impact on spiders.

METHODS

Study orchards.—Sampling was conducted in 42 orchards (apple and pear), all of which were located in Yakima County, Washington. All orchards were within a radius of 46 km of the city of Yakima. Some study orchards have been removed from production since completion of the study. The following are latitudes and longitudes for 8 orchards located at the periphery of the study area: 46.4529°N, 120.2292°W; 46.5029°N, 120.1667°W; 46.5835°N, 120.3501°W; 46.5185°N, 120.4235°W; 46.7432°N, 120.7738°W; 46.6618°N, 120.7557°W; 46.4715°N, 120.3834°W; 46.3106°N, 120.1236°W. All other orchards fell within the area demarcated by the peripheral orchards. Insect pest management in the study orchards ranged from conventional programs based on synthetic, broad-spectrum insecticides (e.g., azinphos-methyl) to state-certified organic programs in which use of synthetic insecticides is prohibited. The codling moth *Cydia pomonella* (Linnaeus 1758) is the key pest of apple and pear in this region.

The study was conducted from 1996 to 2001, but not all orchards were sampled each year. Nine apple orchards were

sampled in 1996. The following year three pear orchards were sampled in addition to the nine apple blocks. The maximum number of orchards sampled in one year was 19 in 1999. Orchard size was 0.5 to 32 ha.

Sampling.—Arboreal spiders were sampled with a beating tray, 0.45 m² in area (Bioquip Products, Gardena, CA). One limb 1–2 m above ground on each of 25 trees (15 trees in 1999) was struck three times with a heavy rubber hose to dislodge spiders. Most specimens were promptly preserved in 70% isopropyl alcohol, but selected specimens were saved and reared (see below). Trees in all parts of an orchard were sampled while walking a winding path. The sampling period usually included April to October. Samples were collected every 1–2 weeks in 1996–1998 and 2000 and monthly in 1999 and 2001. All specimens taken during this study are held at the Yakima Agricultural Research Laboratory (USDA-ARS) in Wapato, Washington, USA.

Sweep net sampling (net diameter = 38 cm) of the understory vegetation was done in 1996 and 1997 in the same orchards that were monitored with beat trays. An 180° swing of the net constituted a sweep, and 25 sweeps per sample were taken while walking a winding path so as to sample in all parts of the orchard. The sampling periods were late June to late October 1996 and mid-May to mid-October 1997. Samples were taken every 1–2 weeks with longer intervals after an orchard was mowed.

Spiders were also collected by hand on an irregular basis when chanced upon or during an occasional more serious search. Generally, one or a few specimens of interest were collected. Immatures were reared to obtain a positive identification if necessary. These data were used to supplement beat tray and sweep net data.

Cardboard shelters of two types were used to collect overwintering spiders. The first consisted of a bundle of ten, 12.5 cm × 17.5 cm sheets of cardboard (flute size ~ 4 mm × 5 mm) tied to the lowest crotch of a tree. The second was a 7.6 cm wide strip of cardboard wrapped once around the trunk of a tree 0.5–1.0 m above ground. Shelters were set out in September and October, retrieved in December or January, and stored in a cold room until processed. The number of shelters set out and the number of orchards sampled varied from year to year.

Incidental to a 1998 study of apple bin use by overwintering codling moth larvae, spiders that had also overwintered in the bins were collected. Bins were removed from the field after harvest, held in a cold room at 0.6°–1.7° C until late January, and then placed in a greenhouse at 21°–24° C. Spiders were collected as they emerged from the bins.

Sample processing.—Selected specimens were reared for positive identification. They were held in 35 ml plastic cups and provided water and prey of appropriate size weekly. Field captured *Lygus* sp. (Hemiptera: Miridae) and laboratory reared *Drosophila* sp. (Diptera: Drosophilidae) were readily consumed by most species. Once a familiarity with the local fauna was acquired it was possible to identify a majority of immatures to species. Specimens of definite developmental stage (e.g., penultimate female, antepenultimate male, etc.) mentioned in Results in all cases refer to reared individuals.

Immatures were sorted into small, medium, and large size classes on a species-by-species basis. Since many spiders pass

through five to seven nymphal instars, this roughly corresponds to instars one, two, and three for small, four and five for medium, and six and seven for large immatures. Although somewhat arbitrary, this allowed an estimate of the age distribution of immatures through the season. Penultimate males were readily distinguished by their enlarged pedipalps. *Theridion*, *Erigone*, and *Meioneta*, because of their small size, were sorted into a single class of immatures, in addition to penultimate males and adults; antepenultimate male *Erigone* and *Meioneta* were distinguishable based on a slight enlargement of the pedipalps.

Data presentation.—Data from beat tray and sweep net collections were combined to obtain monthly totals. These data are presented graphically for eight abundant species to show the proportion of different developmental stages in each month's collection. Note that a small number of beat tray samples (17) were taken during the first week of November. These data were pooled with the extensive October data for the graphs. Few specimens were taken in November because leaf fall was well underway and spiders had begun a general movement out of the trees. Information for less abundant species is summarized in the Tables which also include data from hand collections when available. Overwintering data from all years were combined.

RESULTS

Salticidae.—Adults of both sexes of *Pelegrina aeneola* (Curtis 1892) were abundant in April, May, and June (Fig. 1). Thereafter males were rare although females were present through October. Females with egg sacs were most common during May and June, but an egg sac containing undispersed first instar nymphs was collected as late as 8 September 2000. A female collected with her egg sac on 3 June 1997 produced a second clutch of eggs in the laboratory. Small immatures were present in all months but comprised over 85% of the population in July. Penultimate males and large nymphs, which included penultimate females, were most abundant in October. Large immatures and penultimate males were the principal overwintering stages although small and medium-sized immatures were well represented (Table 1). Penultimate males were uncommon in the trees during April, but five adults hand-collected in the litter in early April 1997 may indicate that many penultimate males undergo their final molt in this location and then move up into the trees. *Pelegrina aeneola* appears to have an annual life cycle in the study area.

The phenology of *Sassacus papenhoei* Peckham & Peckham 1895 was similar to that of *P. aeneola* but lagged about a month behind (Fig. 1). Adults were most abundant during June, and small immatures dominated the population during August. The few individuals found in overwintering refuges were small and medium-sized immatures (Table 1) as were the few specimens taken in beating tray samples during April. An annual life cycle in the study area is indicated for *S. papenhoei*.

Four species of large jumping spiders in the genus *Phidippus* occurred in the orchards. Collection data, summarized in Table 2, indicates annual life cycles for all four but with different maturation times. The first two or three nymphal instars were very similar in appearance and could not reliably be sorted to species. *Phidippus comatus* Peckham & Peckham 1901 matured during the summer. A female guarding her egg

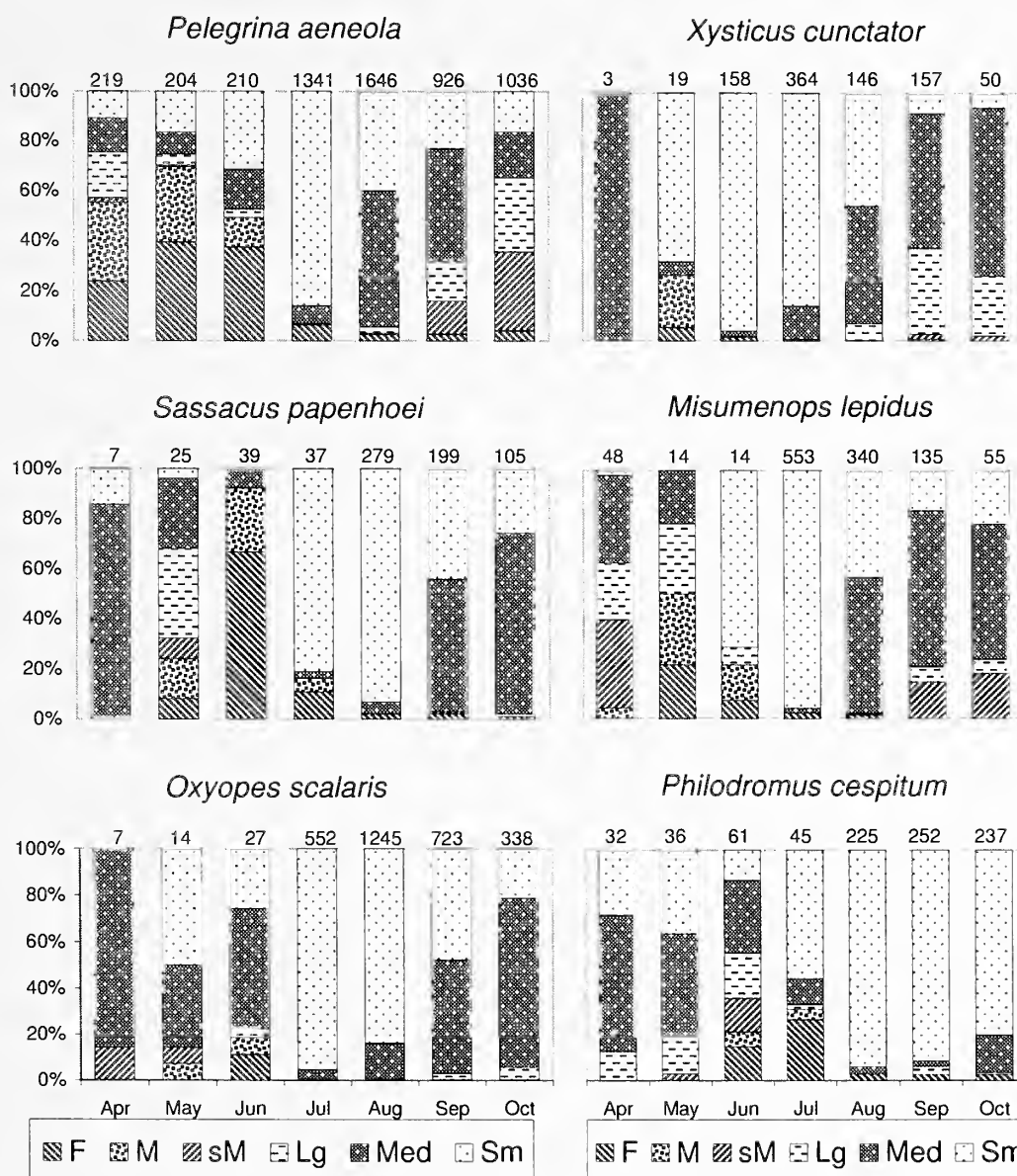


Figure 1.—Percentage of adults and different sized immatures of six common spider species found by month in combined beating tray and sweep net collections. F = female; M = male; sM = penultimate male; Lg = large immature; Med = medium sized immature; Sm = small immature. Number at the top of the column is the total number of specimens taken for the month.

sac was found among a group of ripening pears on 19 August 1998, and a female with a hatched egg mass was found in a codling moth pheromone trap on 29 October 1996. Three small immatures collected on 26 September 2003 yielded a recognizable *P. comatus* after two molts, a male after five molts, and a penultimate female after six molts. *Phidippus clarus* Keyserling 1885 also appears to mature during the summer (Table 2). *Phidippus audax* (Hentz 1845) appears to mature in the spring. Specimens from overwintering shelters (Table 1) were mostly medium and large immatures and, of the 42 individuals that overwintered in apple bins, 26 were penultimate females and 12 were penultimate males. *Phidippus johnsoni* (Peckham & Peckham 1883) also appears to mature in the spring. Overwintering and seasonal collection data for other Salticidae is summarized in Tables 1 and 2 respectively.

Oxyopidae.—*Oxyopes scalaris* Hentz 1845 was infrequently collected from March to June, but its numbers increased

substantially in July and August. Medium-sized immatures made up 50% of the population in September and 73% in October, but large immatures were present in only small numbers both months. Miscellaneous collections included 2 females, 2 penultimate females, and 1 antepenultimate female on 26 May 2000; 1 female and 1 penultimate female on 30 May 2000; and 1 penultimate male on 1 June 2000. *Oxyopes scalaris* appears to mature in the spring and early summer and to be univoltine in the study area.

Thomisidae.—Immature *Xysticus cunctator* Thorell 1877 were commonly taken in the beat tray samples. Adults, however, were rare in the trees (one female out of 609 specimens) but were more frequently swept from the understory vegetation (five males and four females out of 288 specimens). Adults were most numerous in May according to sweep net and beat tray collections, but hand collected adults of both sexes were taken in April. New generation

Table 1.—Summary of spider overwintering stages: sm., med., lg. = small, medium, and large immatures (large immatures included antepenultimates of both sexes and penultimate females); sM = penultimate males; M = adult male; F = adult female. Additional observations: one med. *P. cespitum* molted three times to an adult female; the sm. *P. insperatus* molted four times to a male and seven of the med.'s molted three times each yielding five males and two females; one sM *P. alascensis* was reared to the adult stage.

Spider species	Overwintering stage					
	sm.	med.	lg.	sM	M	F
Salticidae						
<i>Pelegrina aeneola</i> (Curtis 1892)	39	87	227	192	1	1
<i>Sassacus papenhoei</i> Peckham & Peckham 1895	5	5				
<i>Sassacus vitis</i> (Cockerell 1894)	4	3			1	
<i>Phidippus audax</i> (Hentz 1845)	1	10	12	4		
<i>Phantias watonus</i> (Chamberlin & Ivie 1941)	21	49	23	4	10	28
<i>Salticus scenicus</i> (Clerck 1757)	5	24	34	46		1
Oxyopidae						
<i>Oxyopes scalaris</i> Hentz 1845		2				
Thomisidae						
<i>Xysticus cunctator</i> Thorell 1877		1				
<i>Misumenops lepidus</i> (Thorell 1877)	29	48	5	34		
Philodromidae						
<i>Philodromus cespitum</i> (Walckenaer 1802)	310	83	10	1		
<i>Philodromus insperatus</i> Schick 1965	1	9				
<i>Philodromus californicus</i> Keyserling 1884		9	129	1		
<i>Philodromus rufus</i> Walckenaer 1826		25	269	7		
<i>Philodromus speciosus</i> Gertsch 1934		2	10	1	3	5
<i>Philodromus alascensis</i> Keyserling 1884			1	2		
<i>Tibellus oblongus</i> (Walckenaer 1802)	27	16	4			
<i>Ebo pepinensis</i> Gertsch 1933	3	3	2			
Clubionidae						
<i>Cheiracanthium mildei</i> L. Koch 1864	104	210	37	40		
<i>Cheiracanthium inclusum</i> Hentz 1847		1		1		
Corinnidae						
<i>Phrurotimpus borealis</i> Emerton 1911		14	203	140		
Anyphaenidae						
<i>Anyphaena pacifica</i> (Banks 1896)	2	6	6			
Theridiidae						
<i>Steatoda hespera</i> Chamberlin & Ivie 1933	15	31	4	1	3	2
Linyphiidae						
<i>Meioneta fillmorana</i> (Chamberlin 1919)						1
<i>Erigone</i> spp.					1	
<i>Pityohyphantes minidoka</i> Chamberlin & Ivie 1943	11	19	3	1		1
Tetragnathidae						
<i>Tetragnatha laboriosa</i> Hentz 1850	6	1	1			
Dictynidae						
<i>Dictyna coloradensis</i> Chamberlin 1919			35	21	1	

spiderlings appeared in May and remained abundant through August (Fig. 1). Antepenultimate males, as indicated by rearing, were present as early as July. Penultimate females (reared individuals) and penultimate males (Fig. 1) were present by September. Larger immatures, including penultimates of both sexes, would therefore be the primary overwintering stages. This species appears to have an annual life cycle in the study area.

The phenology of *Misumenops lepidus* (Thorell 1877) was similar to that of *X. cunctator* although new generation spiderlings did not appear in large numbers until July (Fig. 1),

a few weeks later than in *X. cunctator*. Penultimate males first appeared in August and were abundant in September, October, and the following April. Penultimate males and other immature stages overwintered (Table 1). *Misumenops lepidus* appeared to have an annual life cycle.

Philodromidae.—The phenology of *Philodromus cespitum* (Walckenaer 1802) (Fig. 1) was similar to that of *X. cunctator* and *M. lepidus* but was shifted later into the season. Adult females were most common in June and July, and small spiderlings, which could be found in all months, were most abundant from August to October. Five females with egg sacs

Table 2.—Summary by month of beating tray, sweep net, and hand collections of less common spider species: numbers of penultimate males, males, and females, respectively, are given. Additional observations: Penultimate female *E. militaris* were collected in April, May, September, and October; two antepenultimate female *X. gulosus* collected in July, one female collected in December; one penultimate female *P. insperatus* collected in June, one female collected in June laid three egg clutches in the lab; one antepenultimate female *P. californicus* collected in April, one antepenultimate female and 26 other large immatures collected in October; three antepenultimate male *A. trifasciata* collected in July and one in August, 2 penultimate females collected in August.

Spider species	April	May	June	July	Aug	Sept	Oct
Salticidae							
<i>Eris militaris</i> (Hentz 1845)	0-2-0	2-2-11	0-0-4	1-0-4	3-0-1	0-1-0	1-3-0
<i>Phanias watonns</i> (Chamberlin & Ivie 1941)				0-0-2			
<i>Phidippus andax</i> (Hentz 1845)		0-1-0	0-0-1	0-1-1	0-0-1		10-0-1
<i>Phidippus clarns</i> Keyserling 1885				1-7-11	0-1-1	0-0-3	0-0-1
<i>Phidippus comatus</i> Peckham & Peckham 1901		1-0-0	9-1-1	1-11-8	0-4-4	0-1-0	0-0-1
<i>Phidippus johnsoni</i> Peckham & Peckham 1883	0-3-2			1-0-0		1-0-0	2-1-0
<i>Sassacus vitis</i> (Cockerell 1894)					0-2-0		
<i>Salticus scenicus</i> (Clerck 1757)		1-0-0	0-1-1				
Thomisidae							
<i>Xysticus gulosus</i> Keyserling 1880				1-0-0		0-0-1	0-1-3
Philodromidae							
<i>Philodromus insperatus</i> Schick 1965		2-0-0	0-2-2	0-0-4			
<i>Philodromus californicus</i> Keyserling 1884							3-0-0
<i>Philodromus rufus</i> Walckenaer 1826		0-2-0					
<i>Tibellus oblongus</i> (Walckenaer 1802)		0-1-2	0-0-1	1-9-9	1-1-7	0-0-1	
<i>Tibellus asiaticus</i> Kulczyn'ski 1908				0-0-1			
Clubionidae							
<i>Cheiracanthium inclusum</i> Hentz 1847		2-1-0			0-0-1		
Corinnidae							
<i>Castianeira longipalpa</i> Hentz 1847				1-0-0			
Anyphaenidae							
<i>Anyphaena pacifica</i> (Banks 1896)			0-0-1	0-0-1		3-0-0	
Linyphiidae							
<i>Spirembolus mundus</i> Chamberlin & Ivie 1933			7-0-0	14-0-0	11-0-0	1-1-0	0-1-0
<i>Tenuiphantes tennis</i> (Blackwall 1852)	0-0-1		0-2-2	0-0-1	0-0-2	0-1-1	0-1-0
<i>Collinsia ksenius</i> (Crosby & Bishop 1928)	0-0-1		0-5-3	0-3-1			0-1-3
<i>Walckenaeria subspiralis</i> Millidge 1983			0-5-0	0-1-0		0-1-0	0-2-4
<i>Pityohyphantes minidoka</i> Chamberlin & Ivie 1943		0-1-0					
Tetragnathidae							
<i>Tetragnatha laboriosa</i> Hentz 1850		5-4-2		0-2-2	4-14-11	1-0-3	1-0-2
<i>Tetragnatha versicolor</i> Walckenaer 1841		0-2-0		0-1-1			
Araneidae							
<i>Argiope trifasciata</i> (Forsskål 1775)				1-0-0	3-1-0	0-0-2	

were collected in July, and a female with an egg sac containing undispersed spiderlings was found in September. Small and medium sized immatures most commonly overwintered (Table 1), and an annual life cycle in the study area is indicated.

Tibellus oblongus (Walckenaer 1802) occurred in many orchards. While primarily an inhabitant of the understory vegetation (212 of 256 specimens), individuals were occasionally found in the trees. It overwintered as immatures of various sizes (Table 1) and is probably univoltine in the study area. Overwintering and seasonal collection data for less common species in the Philodromidae are given in Tables 1 and 2 respectively.

Clubionidae.—*Cheiracanthium mildei* L. Koch 1864 occurred in many study orchards and appears to have an annual life cycle in the study area. Collection data for the species are

summarized in Table 3. All sizes of *C. mildei* immatures overwintered including penultimate males and females (Table 1). *Cheiracanthium inclusum* Hentz 1847 was collected in only one of our study orchards but appears to have a phenology similar to that of *C. mildei*. Small immatures were most abundant in July (15 specimens) and August (20), medium-sized immatures were most abundant in September (19) and October (17), and large immatures were most abundant in October (13).

Theridiidae.—*Theridion neomexicanum* Banks 1901 was a common, primarily arboreal species that is clearly univoltine in the study area (Fig. 2). Males were first noted in May, but both sexes were most abundant in June and July. A male and a penultimate female were found together in a web on an apple leaf on 11 June 1998, females with egg sacs were collected on apple leaves on 10 July 1998 and 27 July 1999, and a female

Table 3.—Seasonal occurrence of *Cheiracanthium mildei* based on combined beat tray, sweep net, and hand collections. Spider stages: small, medium, large = small, medium, and large immatures (large immatures included antepenultimate nymphs of both sexes and penultimate females); sM = penultimate males. Additional observations: two of the July and one of the September females were guarding egg sacs.

Month of collection	Developmental stage					
	small	medium	large	sM	Male	Female
May	1			1	1	
June		1	1			1
July	28	5	3		1	3
August	29	28	2			
September	18	29	14	5		3
October	19	44	23	10		

with a vacated egg sac was found on 6 August 1999. Penultimate males were not observed by October, and overwintering must therefore occur as immatures smaller than penultimates in undetermined locations.

Linyphiidae.—*Meioneta fillmorana* (Chamberlin 1919) is also primarily an arboreal spider. Its numbers peaked in May, after which there was a four month decline and then a marked rebound in October. Such a late season increase was unusual for spiders in this study especially since the October population of *M. fillmorana* consisted entirely of adults (Fig. 2). Six years of beat tray samples all showed a similar pattern, however. The species appears to be univoltine. Although we obtained virtually no overwintering data for *M. fillmorana*, it seems reasonable to infer, given the preponderance of females in the October collections, that overwintering probably takes place in the egg stage.

At least two species of *Erigone* occurred in the orchards: *Erigone dentosa* O. Pickard-Cambridge 1894 and *Erigone aletis* Crosby & Bishop 1928. We were unable to separate the two species with certainty. Adults of both sexes were present from at least May to October and were most abundant in October and June (Table 4). Although *Erigone* were well represented in the trees, sweep samples for 1996 and 1997 yielded a majority (65%) of the specimens that were collected. *Erigone* is also common on the ground based on pitfall trap collections (Miliczky et al. 2000), and thus has a broad distribution among habitats within the orchard. Tables 1 and 2 have data for less common Linyphiidae.

Other families.—Data for less commonly collected spiders in other families is summarized in Tables 1 and 2. Included in this group: *Anyphaena pacifica* (Banks 1896) (Anyphaenidae) was occasionally found in the trees and immatures utilized overwintering shelters; *Tetragnatha laboriosa* Hentz 1850 (Tetragnathidae) was commonly swept from understory vegetation, and immatures were taken with some regularity in late season beat trays; *Dictyna coloradensis* Chamberlin 1919 (Dictynidae) was common only at the USDA research farm where it constructed webs on apple and pear leaves and tall weeds in adjacent uncultivated ground.

DISCUSSION

Many temperate zone spiders have a single generation per year (Gertsch 1979; Foelix 1996), and this appeared to be true

of Washington species for which sufficient data were obtained. Within the broad latitudinal range of the temperate zone, however, factors that may influence spider development vary widely, and other life history patterns have been documented. About half of the 52 species studied in Denmark by Toft (1976, 1978) were biennial, and Almquist (1969) found a similar proportion of biennial species among 20 studied in Sweden. Almquist (1969) also observed that in Sweden the life cycles of some species were twice as long as the life cycles of the same or related species in southwestern Europe. Similarly, *Philodromus cespitum* is biennial in Nova Scotia (Dondale 1961) but univoltine farther to the south in Ontario (Putman 1967).

In North America and Denmark maturation times among univoltine spiders form a continuum from the spring to the fall (Toft 1976; Gertsch 1979). Some litter inhabiting species of Linyphiidae mature and reproduce even during the winter months (Duffey 1956; Schaefer 1977). Washington species for which we acquired sufficient data appeared to have well-defined periods of reproduction (stenochrony) and could be classified as stenochronous with reproduction in spring and summer (Schaefer 1977).

We noted that at a given time during the season, and also in the overwintering shelters, some species were represented by several developmental stages, whereas others were represented by only a few. Small, medium, and large immature *Pelegriana aeneola* could be found during much of the season (Fig. 1) and all these stages also overwintered (Table 1). *Cheiracanthium mildei* showed a similarly broad range of overwintering stages, while *Phanias watomus* was even more extreme as adults of both sexes also commonly overwintered (Table 1). In contrast, small immature *Philodromus cespitum* dominated the orchard collections from August to October (Fig. 1) and was the principal overwintering stage (Table 1). *Philodromus californicus* and *Dictyna coloradensis* spent the winter primarily as large immatures and/or penultimate males and penultimate females (Table 1). Factors tending to increase the length of time during the season when a given developmental stage is present include long-lived females that remain with an egg sac until the young disperse and produce more than one clutch of eggs. Egg sac guarding by *P. aeneola* was observed in the field, egg sacs were found as late as September, and females are capable of producing a second clutch of eggs. *Pelegriana galatea* (Walckenaer 1837) also guarded its eggs and produced multiple clutches in the laboratory (Horner & Starks 1972). We observed female *C. mildei* guarding eggs in the field and multiple clutches of eggs were produced under laboratory conditions (Mansour et al. 1980b).

A number of the more common orchard spiders were poorly or not at all represented in overwintering shelters and presumably seek alternative sites inside or outside the orchard. Pekar (1999c) noted a similar phenomenon. *Oxyopes scalaris*, the only member of the family that occurs in Washington (Crawford 1988), presented an interesting case. Large numbers of small immature *O. scalaris* appeared in the orchards rather abruptly in July, and size increase in the population was observed as the season progressed. Large immatures and adults were rare in orchard collections (Fig. 1), however, and only two immatures were found in overwintering shelters (Table 1). The fate of the medium sized immatures that are so

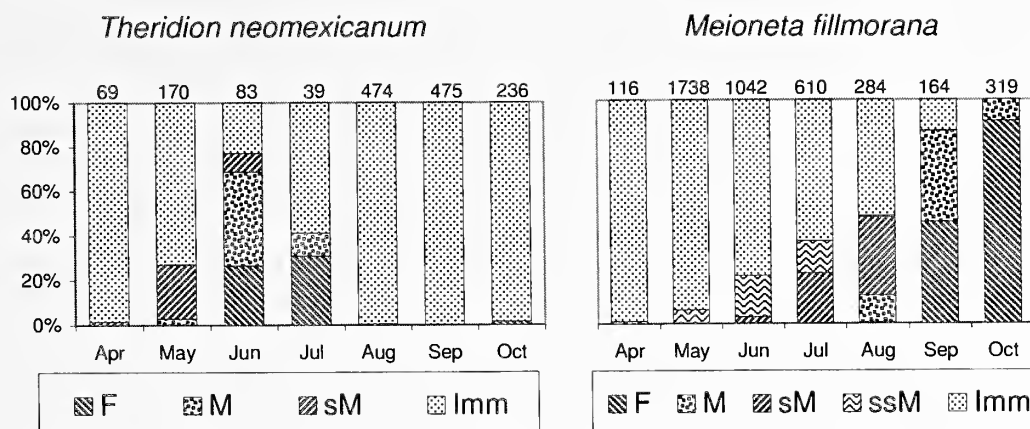


Figure 2.—Percentage of adults and immatures of two common spider species found by month in combined beating tray and sweep net collections. F = female; M = male; sM = penultimate male; ssM = antepenultimate male (*M. fillmorana* only); Imm = all other immature stages. Number at the top of the column is the total number of specimens taken for the month.

common in the orchards in October remains to be determined. The opposite situation was noted in *Steatoda hespera* which utilized overwintering shelters but was not taken by beating tray or sweep net. Like most members of the genus, *S. hespera* webs are probably situated in rock and bark crevices and in cavities near the ground (Levi 1957) and would not have been sampled. Horton et al. (2001) changed a portion of their cardboard bands on pear and apple trees weekly from August to December. They determined that several species utilized the bands as temporary refuges during the autumn but overwintered elsewhere.

Despite their abundance in terrestrial habitats and their exclusively predatory habits, Debach & Rosen (1991) noted a general neglect of spiders as potential biological control agents and attributed this, in part, to their generalist predatory habits. Other authors, noting the diversity of prey capture strategies and microhabitat exploitation patterns of spiders, have emphasized the contribution of the spider community as a whole to insect control in agroecosystems (Reichert & Lockley 1984; Marc & Canard 1997). Interest in the composition of spider faunas in orchards began over 50 years ago and appears to have increased given the number of studies conducted in recent years. However, studies attempting to evaluate the importance of spider predation on orchard pests are few (e.g., MacLellan 1973; Mansour et al. 1980a; Amalin et al. 2001; Miliczky & Calkins 2002).

Table 4.—Summary by month of combined beating tray and sweep net collections of *Erigone* spp. Spider stages: ssM = antepenultimate male; sM = penultimate male.

Month of collection	Developmental stage			
	ssM	sM	Male	Female
April	4			1
May	40	28	4	6
June	19	59	71	53
July	49	68	23	14
August	24	35	23	14
September	43	50	34	22
October	2	32	192	197

During this study we observed most of the common orchard spiders feeding on pests. *Pelegrina aeneola*, *O. scalaris*, *P. cespitum*, *X. cunctator*, and *M. lepidus* all used a variety of smaller pest species as prey, including leafhoppers, leafminers, aphids, thrips, and mites. The webs of *M. fillmorana* snared aphids and thrips as well as tiny flies and parasitoid wasps. The large salticid *Phidippus clarus* took prey up to the size of an adult earwig. Some of the orchard spiders or a close relative may be important predators in agroecosystems more generally. *Pelegrina aeneola* and other members of the genus may be important in biological control because they are often abundant and are known to feed on pest insects (Horner 1972; Jennings & Houseweart 1978; Mason & Paul 1988). *Oxyopes salticus* Hentz 1845, a close relative of *O. scalaris*, is a dominant predator in row crops in the United States and an important predator of pest insects (Young & Lockley 1985). *Cheiracanthium mildei* was described by Wise (1993) as a potentially important biological control agent in a number of agroecosystems. Mansour et al. (1980a) determined that *C. mildei* was the most effective spider predator of a lepidopteran pest of apples in Israel. Miliczky & Calkins (2002) rated it as having the greatest potential as a predator of pest leafrollers in Washington orchards out of 11 species tested.

The role of spiders in orchard pest control is of considerable interest given the current trend toward reduced use of broad spectrum insecticides, the large numbers of spiders often observed when pesticide use is decreased or eliminated, and the great diversity among orchard-inhabiting spiders in size, behavior, and prey-capture strategies. All of these factors suggest that spiders should have substantial potential for contributing to orchard pest control. Future studies should further document the importance of this interesting but often overlooked group of beneficial organisms in controlling pest species in orchards and other agricultural systems.

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Distribution of *Geraecormobius sylvarum* (Opiliones, Gonyleptidae): Range modeling based on bioclimatic variables

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Abstract. The potential distribution of the harvestman *Geraecormobius sylvarum* Holmberg 1887 (Opiliones, Gonyleptidae, Gonyleptinae) from Argentina, Brazil and Paraguay, is modeled using the presence-only, GIS-based method BIOCLIM. The model was run on 2.5 min resolution climate layers using 19 derived bioclimatic variables. The bioclimatic profile of the species is described, and presumable limiting factors in each part of the range are discussed. Modeled distribution of *G. sylvarum* shows a remarkable correspondence to the Alto Paraná Atlantic forest ecoregion, with a marginal presence around the *Araucaria* forests and in gallery/flood forests towards the Southwest. Results support the 650 km yungas-Mesopotamia disjunction, as previously proposed, and reveal that localities in northwestern Argentina have extreme values concerning seasonality parameters with remarkably decreased rainfall in winter. Evidence suggesting that the disjunct pattern may have been derived by anthropic introduction is briefly discussed.

Keywords: Neotropics, BIOCLIM, potential distribution, ecological niche modeling, environmental envelope

Harvestmen (Arachnida, Opiliones) are generally regarded as a well suited taxon for biogeographic studies (Ringuelet 1959; Giribet & Kury 2007). Two key features make them useful for those purposes: their low vagility and a close dependence on environmental conditions, mainly humidity (Acosta 2002; Pinto-da-Rocha et al. 2005; Machado et al. 2007). Distribution of most species is thus dependent on the geographic continuity of suitable environments (Acosta 2002). In addition, harvestman endemism may be particularly remarkable in some areas (Machado et al. 2007). Small-area endemism is striking in forested ranges like the Brazilian Serra do Mar (Pinto-da-Rocha et al. 2005), and is also important in the montane forests of northwestern Argentina, the so called “yungas” region (Acosta 2002).

However, small-ranged endemics should not be seen as the rule for harvestman distribution. Under certain conditions, many species are known to spread over thousands of km² (Curtis & Machado 2007) as long as the suitable environment is not restricted by any geographic or ecological barrier. For example, while many central European species appear geographically restricted, no less than 30 harvestmen in that region extend over quite large ranges (Martens 1978). Broad ranged species are also typical for most of the Argentinean Mesopotamia, which is the humid and sub-humid region between the Paraná and Uruguay rivers (Acosta 2002). Its northernmost portion, roughly matching the administrative province of Misiones, bears subtropical forest physiognomy - actually a part of the “Paranense Biogeographic Province” (Cabrera & Willink 1973) that covers adjacent areas in Paraguay and Brazil as well. The rest of Mesopotamia is a mosaic of shrubs, swamps, grasslands and gallery forests (Hueck & Seibert 1972; Cabrera & Willink 1973). In accordance with these differences, the Mesopotamian opilofauna has been split into two different, though overlapping, sub-areas (Acosta 2002): the Misiones sub-area and the Mesopotamian *sensu stricto* sub-area. Towards the West, as precipitation decreases, these humid and sub-humid realms give way to the semiarid Chaco, an effective distributional limit for Mesopotamian harvestmen (Acosta 2002).

Geraecormobius sylvarum Holmberg 1887 (Opiliones, Gonyleptidae, Gonyleptinae) is a large and conspicuous harvestman known to inhabit subtropical forests in north-eastern Argentina, southern Brazil and southeastern Paraguay (Ringuelet 1959; Kury 2003; Acosta et al. 2007), being thus characteristic of the Misiones sub-area (Acosta 2002). Acosta et al. (2007) provided several new records for this species; among them three localities in the province of Tucumán, Argentina, revealing a disjunct presence in montane forests in northwestern Argentina (NWA). These separate populations lie about 650 km away from the westernmost record in the core area, with the sub-xeric Chaco in between. As stressed by Acosta et al. (2007), most records of *G. sylvarum* concentrate in the Alto Paraná Atlantic forests ecoregion (referred to as “Paranense forests” below) and in some adjacent sectors of the *Araucaria* moist forest ecoregions (nomenclature after Olson et al. 2001). Argentinean captures outside the mentioned ecoregions (in provinces of Corrientes and Chaco) seemingly are associated with gallery forests and/or seasonal inundation sites (the Humid Chaco and Southern Cone Mesopotamian savanna ecoregions of Olson et al. (2001)). In turn, findings of *G. sylvarum* in NWA correspond to the “tucumano-boliviano” forests, or “yungas” (Hueck & Seibert 1972; Acosta 2002), or the Southern Andean Yungas ecoregion (Olson et al. 2001). The available localities show some spatial bias, since they are concentrated in and around the province of Misiones (a traditionally well sampled area; Ringuelet 1959), while extensive areas in Paraguay are left almost undocumented (cf. Fig. 3).

Interestingly, two further Mesopotamian harvestmen, *Discoerytus dilatatus* Sørensen 1884 and *D. prospicius* (Holmberg 1876) (Gonyleptidae, Pachylinae) have Mesopotamia-yungas disjunct ranges as well (Acosta 1995, 2002). A very basic question remains unanswered, however: Are Chacoan conditions really inhospitable to Mesopotamian species or is our record incomplete, leading us to wrongly assume this region to be hostile for harvestmen? Nothing is known about the climatic tolerances of *D. dilatatus*, *D. prospicius* or *G.*

sylvorum as very little is known about harvestmen physiology and tolerance to physical factors in general (Santos 2007). It is generally accepted that harvestman distribution is governed by climatic constraints, mainly humidity and temperature, but papers addressing how actual climatic conditions affect a given species are almost lacking (Curtis & Machado 2007; Machado et al. 2007).

The occurrence records contain some useful clues. Point records are the very basis for discovering a species range, though the vast majority of Neotropical harvestmen have been scarcely recorded, so that species with more than 15 records are rare (cf. Kury 2003). In fact, most distributional patterns are then intuitively extrapolated from the few records available, emphasizing the need for gathering more data and filling in the gaps. Alternatively, recent developments aimed to model potential species ranges, using available records and several types of environmental predictors, offer innovative methods to help detect areas where presence of a given species may be expected though still not documented (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Hernández et al. 2006; Peterson 2006). Using a Geographic Information System (GIS) and appropriate climate information, the envelope approach infers the species' bioclimatic profile, a species-specific feature (actually, a subset of the fundamental ecological niche) that gives us a rough insight into their presumed tolerance limits, at least with respect to the variables used to build the model. It is then possible to project this profile onto the geographic space, to identify all areas with similar climatic conditions, i.e., where the species would meet a potentially suitable environment (Guisan & Zimmermann 2000; Hijmans & Graham 2006; Hernández et al. 2006; Pearce & Boyce 2006). This paper is intended to characterize the bioclimatic profile of *G. sylvorum* and to model its potential distribution using the BIOCLIM algorithm, taking advantage of the number of records now available for this species (close to the minimum sample size for the method to attain an acceptable accuracy; Hernández et al. 2006). Thereby it is also intended to test if the disjunct Mesopotamian-yungas pattern is supported by the model and to identify areas in which future sampling efforts would be productive in filling in distribution gaps. Results are matched to major biomes and habitat types in order to get a more comprehensive understanding, though still preliminary, of the ecological requirements and potential range of this wide-ranged harvestman.

METHODS

Data acquisition.—All published references for *G. sylvorum* were taken into account (Holmberg 1887; Ringuet 1959; Soares & Soares 1985; Kury 2003; Acosta et al. 2007). Historical records were inspected for taxonomic reliability (cf. Acosta et al. 2007 for localities excluded), while three localities from the province of Misiones (published by Ringuet 1959) remained unrecognizable and were set aside: "Campamento Yacu-Poi, near Puerto Bemberg"; "60 km Puerto Iguazú" (which direction?), and "Pasarela Río Uruguay." The full dataset consisted of 48 unique point localities; during the analysis, duplicate records from the same gridcell were removed by the software, resulting in 46 effective records. Localities were identified and geo-referenced using printed

road maps and digital gazetteers (mainly NGA GEOnet Names Server [GNS], United States Board on Geographic Names; Google Earth ©), all cross-checked for final accuracy. The label data or collector's information was used to determine location as precisely as possible. Published records typically refer to a locality, which may represent not more than the nearest reference to the actual collecting site; such an imprecision in coordinates (impossible to measure) is deemed not to affect the results considering both the regional scale and coarse approach used.

Climate layers.—The model was run on Worldclim 1.4. (Hijmans et al. 2005a), a set of global climate layers, containing extrapolated monthly data for the 1950–2000 period on maximum, minimum and mean temperature, and precipitation. The 2.5 min resolution (i.e., approximately 4.5 x 4.5 km gridcell) was selected. Information contained in Worldclim (climate data, together with a digital elevation model) is used by the software to derive the 19 bioclimatic variables available for modeling, listed in Table 1. The abbreviation "bc" followed by a number is used below to identify each of these bioclimatic variables.

Modeling method.—Modeling was performed through the presence-only method BIOCLIM, as implemented in Diva-Gis 5.4 (Hijmans et al. 2005b). BIOCLIM is a frequency distribution-based algorithm, which calculates the envelope that bounds the bioclimatic preferences of the species (Fischer et al. 2001; Walther et al. 2004; Hernández et al. 2006). Values of each derived bioclimatic variable are extracted from all localities and arranged in a cumulative frequency distribution (cf. Fig. 2). The envelope is defined as a multi-dimensional hyper-box (each variable representing a dimension) delimiting, at a given percentile, the climatic conditions in the occurrence localities (Guisan & Zimmermann 2000). This set of values constitutes the bioclimatic profile of the species (Fischer et al. 2001), as summarized for the target species in Table 2. In the potential distribution maps (Figs. 1, 4–5), gridcells are scored as suitable (if within the envelope; i.e., the presence of the species can be expected) or unsuitable (outside the envelope). User-defined percentiles were set to define the extent of the envelope (as cut-off) or to rank the gridcells suitability (Fischer et al. 2001; Hijmans et al. 2005b; Hernández et al. 2006).

Evaluation.—The accuracy of the predictive range generated by the model was assessed by calculating the AUC (area under curve) in a receiver operating characteristic (ROC) plot, and the maximum Kappa (max- κ) value, both analyses made in Diva-Gis (Hijmans et al. 2005b). In this study, 70% of the original points were randomly resampled as training data to perform 20 repetitions of the model. Test data included pseudo-absence points selected at random from the background. ROC/max- κ were calculated against the grids stack (0–100 percentile) of the 20 range polygons that were modeled using the training points. AUC values over 0.8 are deemed to reflect a "good" model performance; above 0.9 the accuracy is considered "high" (Luoto et al. 2005). In turn, max- κ over 0.4 are deemed to be "good" and "excellent" if above 0.75 (Randin et al. 2006).

Input variants.—A separate run was performed with records from NWA removed to verify if the species is still predicted in that area. To identify the factors limiting the distribution, the

Table 1.—Median, minimum and maximum values, and range for all 19 bioclimatic variables in the envelope of *Geraecormobius sylvarum*. Absolute temperature values are in degrees Celsius ($^{\circ}$ C), precipitation in mm. Numbers preceding each variable are referred to in the text and Table 2. Main differences between profiles with and without yungas records are emphasized in bold.

Bioclimatic variables	All records ($n = 46$)		Yungas removed ($n = 44$)	
	Median	Min-max (range)	Median	Min-max (range)
(1) Annual mean temperature	20.39	16.46–23.12 (6.66)	20.62	16.46–23.12 (6.66)
(2) Mean monthly T° range	12.43	10.65–13.83 (3.18)	12.43	10.65–13.83 (3.18)
(3) Isothermality ($2/7 \times 100$)	56.08	47.25–65.00 (17.75)	56.21	49.48–65.00 (15.52)
(4) T° seasonality ($STD \times 100$)	368.87	252.92– 461.59 (208.67)	366.90	252.92– 430.76 (177.84)
(5) Max T° of warmest month	31.65	27.20–34.20 (7.00)	31.70	27.20–34.20 (7.00)
(6) Min T° of coldest month	9.25	4.80–12.50 (7.70)	9.40	4.80–12.50 (7.70)
(7) T° annual range (5–6)	22.50	19.00–25.40 (6.40)	22.45	19.00–24.30 (5.30)
(8) Mean T° wettest quarter	21.52	16.20–25.23 (9.03)	21.36	16.20–25.23 (9.03)
(9) Mean T° driest quarter	16.84	13.40–19.22 (5.82)	16.92	14.03–19.22 (5.18)
(10) Mean T° warmest quarter	24.76	20.33–27.58 (7.25)	24.89	20.33–27.58 (7.25)
(11) Mean T° coldest quarter	16.01	12.35–18.50 (6.15)	16.03	12.50–18.50 (6.00)
(12) Annual precipitation	1723.5	934 –2235 (1301)	1730.5	1250 –2235 (985)
(13) Precipitation wettest month	188.5	157–245 (88)	186	157–245 (88)
(14) Precipitation driest month	99.5	11 –150 (139)	101	42 –150 (108)
(15) Precipitation seasonality (CV)	20.34	9.42– 83.74 (74.32)	19.94	9.42– 41.88 (32.46)
(16) Precipitation wettest quarter	495.5	432–625 (193)	495.5	432–625 (193)
(17) Precipitation driest quarter	344.5	40 –496 (456)	349.5	140 –496 (356)
(18) Precipitation warmest quarter	457	354–625 (271)	455	354–625 (271)
(19) Precipitation coldest quarter	360	40 –540 (500)	362	140 –540 (400)

model (full dataset) was alternatively run for each variable separately and combining some of them so as to visually inspect the effects on the resulting predicted range.

RESULTS

Bioclimatic profile.—Table 1 summarizes values relevant to the bioclimatic tolerance range of *G. sylvarum*. Separate profiles with and without the Tucumán localities are given from which it is clear that, for some variables, conditions in the yungas suggest differences from the core area (cf. Table 2 also). Sites from Tucumán represent both the westernmost records and the highest elevation. In those localities precipitation (bc12) is the lowest (Fig. 2B), with rainfall decreasing substantially during the winter (Fig. 2D). There, seasonality is higher than in sites of the core area (Figs. 2A, C); in particular, precipitation seasonality (bc15) is strongly skewed to low values, with both Tucumán records clearly separated by a decided gap from the rest (Fig. 2C). When these localities of NWA are set aside, Rio Tragadero and 10 km Puerto Antequera (close to each other) become the species' westernmost edge and come to hold many of the bioclimatic extremes related to seasonality and winter decrease of precipitation (Table 2 and Fig. 3). However, geographically extreme localities did not necessarily hold the highest or lowest bioclimatic values in all cases (Table 2). Other localities with many bioclimatic variables showing extreme values are Clevelândia (Santa Catarina, Brazil) and Asunción (Paraguay). Clevelândia has nine end values indicating, in general, a cooler and more humid climate than the rest; in turn, Asunción stands as the warmest site of the species range, with highest values for six variables, all temperature-related. With respect to the resulting envelope, a permissive percentile cut-off of 0.005 allowed 33 out of 46 observations (71.7%) to be included within all possible 171 bidimensional envelopes (the remaining 13 observations being outsiders in at least one

bidimensional envelope). With the default percentile of 0.025, localities within the species envelope are reduced to 21 out of 46 observations (45.7%).

Potential range.—The predicted range of *G. sylvarum* under the model parameters is displayed in Fig. 1. To a great extent, the predicted core area of *G. sylvarum* roughly matches the Paranense forests ecoregion (Fig. 3). In eastern Paraguay, where records are almost lacking, the prediction partially redraws the boundaries of this ecoregion with the contiguous Humid Chaco (Fig. 3). On the Brazilian side, the predicted range seemingly enters the *Araucaria* forests only marginally, i.e., in areas surrounded by complex eastward Paranense projections that follow large rivers. A large portion of the *Araucaria* ecoregion is scored as unsuitable; moreover, it is to be noted that Clevelândia, one of the localities with many bioclimatic extreme values (Table 2), is placed near this presumable distributional limit (Fig. 3). In Brazil the modeled range reaches up to the southern states of Mato Grosso do Sul and São Paulo in the North (though with no records so far), and weakly up to the western slopes of the Serra do Mar in the East (Fig. 1). *Geraecormobius sylvarum* was not hitherto collected in the eastern slopes of the Serra do Mar; probably replaced there by its congener *Geraecormobius rohri* (Mello-Leitão 1933) (A.B. Kury, pers. comm.). On the other side, occurrences of *G. sylvarum* in the northern province of Corrientes and eastern Chaco give support to the potential areas southwest of the paranense forests. Subtropical vegetation partially extends into northern Corrientes, as well as along flood and gallery forests along the Paraná and Paraguay rivers (Hueck & Seibert 1972), and this seems to provide suitable conditions for *G. sylvarum* some hundreds of kilometers away from the main range.

With the full dataset, the bioclimatic model predicts the presence of *G. sylvarum* in the yungas but not across the sub-xeric Chaco (Fig. 1); thus, the presumed disjunction is

Table 2.—Localities of *Geraecormobius sylvanum* that represent extreme values, either for geographical coordinates (underlined) or for bioclimatic (bc) variables (numbers as identified in Table 1). Latitude and longitude are given in degrees. Diva-Gis treated the first and second localities as a single point record. In brackets, extreme values of longitude and bc variables if records from Tucumán are removed.

Country	State or Province	Locality	Longitude (W)	Latitude (S)	bc variables, lowest	bc variables, highest	Source
Argentina	Tucumán	Between Cristo and Villa Nougés	<u>-65.3583</u>	-26.8083	3, 11	15	Acosta et al. 2007
Argentina	Tucumán	Road to Cerro San Javier, 700 m	<u>-65.3417</u>	-26.8000	3, 11	15	Acosta et al. 2007
Argentina	Tucumán	El Corte (500–700 m)	-65.3333	-26.8083	9, 12, 14, 17, 19	4, 7	Acosta et al. 2007
Argentina	Chaco	Río Tragadero	(<u>-58.8667</u>)	-27.4333	(3, 14, 17, 19)	(15)	Acosta et al. 2007
Argentina	Chaco	10 km Puerto Antequera	-58.8000	-27.3833	(14, 17, 19)	—	Acosta et al. 2007
Argentina	Corrientes	Laguna Iberá (Iporá)	-57.1833	<u>-28.5167</u>	18	(4)	Ringuelet 1959
Argentina	Misiones	Santa Ana	-55.6000	<u>-27.3667</u>	(12)	—	Holmberg 1887
Argentina	Misiones	Puerto Rico	-55.0333	-26.8000	16	—	Ringuelet 1959
Argentina	Misiones	Salto Encantado	-54.8333	-27.0667	8	—	Acosta et al. 2007
Argentina	Misiones	Piray Mini	-54.6667	-26.3667	—	(7)	Holmberg 1887
Argentina	Misiones	Puerto Bemberg (Pt. Libertad)	-54.6167	-25.9167	—	2 (7)	Ringuelet 1959
Paraguay	Central	Asunción	-57.6333	-25.3000	—	1, 5, 6, 8, 10, 11	Ringuelet 1959
Brazil	Paraná	Clevelândia, Fazenda Tunas	-52.3667	-26.4000	1, 5, 6, 10 (11)	12, 13, 16, 18, 19	Acosta et al. 2007
Brazil	Paraná	Paranavai	-52.4667	<u>-23.0833</u>	13	—	Acosta et al. 2007
Brazil	Paraná	Cavituina, Fazenda Tocantins	-51.3667	-23.3000	4, 7	3	Acosta et al. 2007
Brazil	Paraná	Guaraúna	-50.3667	-25.3333	5 (9)	—	Kury 2003
Brazil	Paraná	Cachoeirinha (nowadays Arapotí)	<u>-49.8217</u>	-24.1533	—	—	Soares & Soares 1945
Brazil	Santa Catarina	Nova Teutônia	-52.4000	-27.0500	—	14, 17	Acosta et al. 2007
Brazil	Rio Grande do Sul	Iraí	-53.2500	-27.2000	15	—	Tavares 1980
Brazil	Rio Grande do Sul	São Valentim	-52.5333	-27.5500	2, 7	9	Tavares 1980
Brazil	Rio Grande do Sul	Gaurama	-52.0867	-27.5867	—	9	Acosta et al. 2007

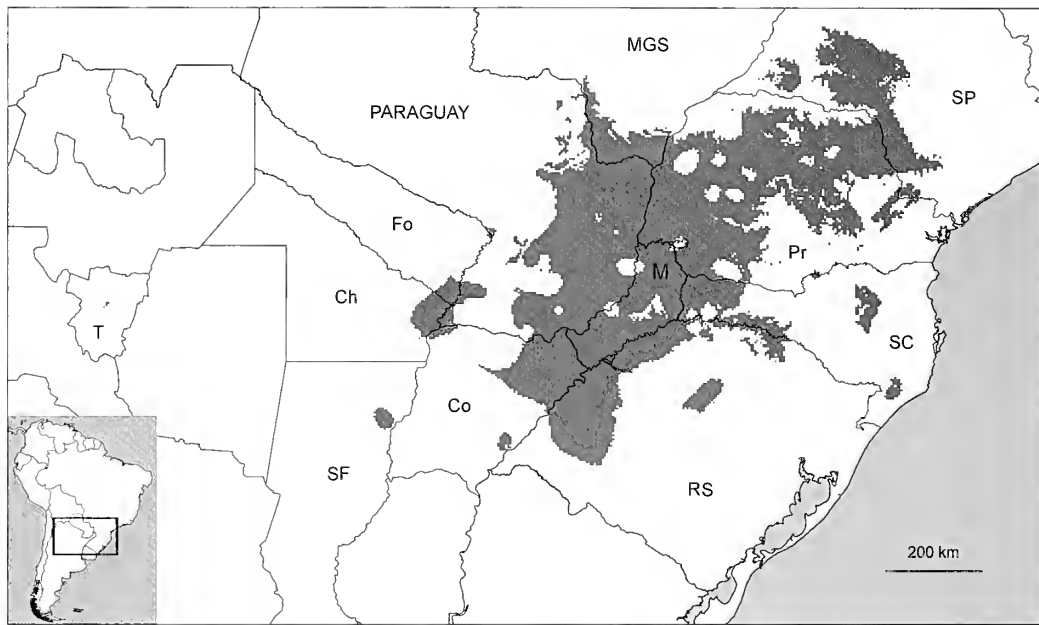


Figure 1.—Predicted range (0-100 percentile) of *Geraecormobius sylvarum* Holmberg, as modeled with BIOCLIM, using the full data set and all 19 bioclimatic variables. Provinces in Argentina: T, Tucumán (detailed map in Fig. 4); Fo, Formosa; Ch, Chaco; SF, Santa Fe, Co, Corrientes; M, Misiones. States in Brazil: RS, Rio Grande do Sul, SC, Santa Catarina, Pr, Paraná, SP, São Paulo, MGS, Matto Grosso do Sul.

supported. However, the probability assigned by the model for its occurrence in Tucumán is very low. Even in a 0–100 percentile envelope, suitable gridcells are few (just four), and if ranked, they fit in the lowest percentile levels (Fig. 4A). With a

0.025 cut-off, no suitable gridcell remains in NWA. As expected by these results, modeling with Tucumán records removed did not predict the species there either. Otherwise, modeling the range without these NWA records had minimal

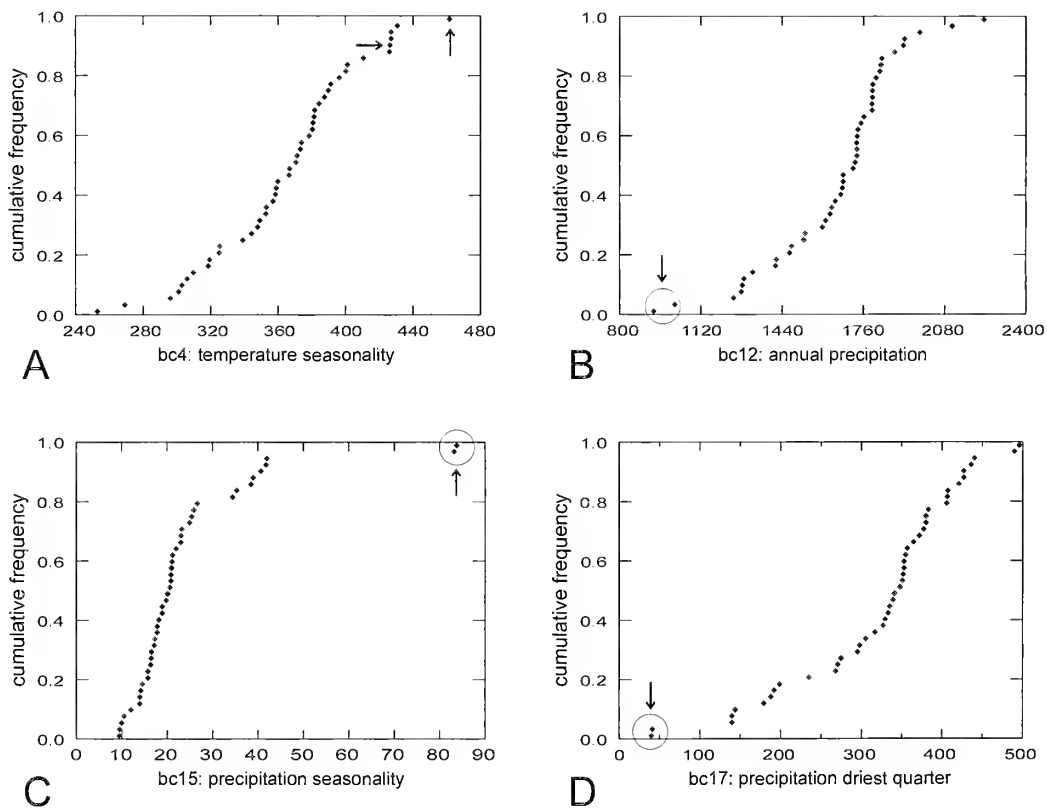


Figure 2.—Bioclimatic profile of *Geraecormobius sylvarum*, selected variables: full data set plotted for cumulative relative frequency; arrows indicate the position of the two localities from province of Tucumán (NWA). A: bc4 – temperature seasonality (standard deviation x 100); B: bc12 – annual precipitation (mm); C: bc15 – precipitation seasonality (coefficient of variation); D: bc17 – precipitation of the driest quarter (mm).

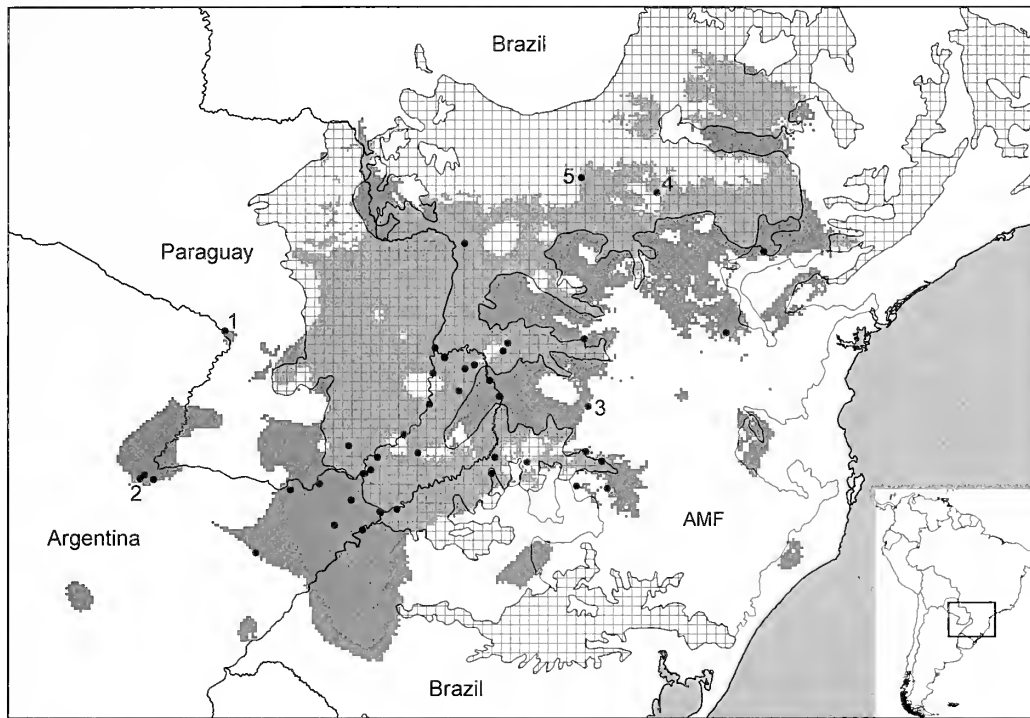


Figure 3.—Correspondence of the modeled range of *Geraecormobius sylvarium* (grey area, 0–100 percentiles) and the Alto Paraná Atlantic forests ecoregion (squared pattern fill); the overlap is shown as a lighter grey squared area. AMF: *Araucaria* moist forests (bordered by a thin line), where *G. sylvarium* is predicted to occur marginally. Dots: all locality records for the species. References of selected localities: 1: Asunción; 2: Río Tragadero; 3: Clevelândia; 4: Caviúna; 5: Paranavaí.

effects in the core area: just a small clipping occurs, reducing the range on marginal sides, like the Corrientes-Chaco portions, and its northernmost extension in Brazil.

Limiting factors.—Models of *G. sylvarium* run separately, with either temperature (bc1–11) or precipitation (bc12–19) variables, uncover the relative contribution of these variables to the predicted range shape. Prediction based on temperature variables bc1–bc11 (Figs. 4B, 5A) more closely recovers the model obtained by all 19 variables together, with a slight “permissiveness” in the southernmost border (province of Corrientes) and especially in NWA (patchy suitable areas appear along the yungas in Tucumán, Jujuy, Salta, and southern Bolivia). Precipitation variables bc12–bc19 (Figs. 4C,

5B) clip most of these areas away from the model, but, in turn, extend suitable conditions considerably eastwards and northwards. In fact, many precipitation variables (when run alone) predict *G. sylvarium* in the yungas, but almost all prevent it entering the Chaco, some being more rigorous (bc15, bc16, bc18), others more “permissive” (bc12, bc14, bc17, bc19); only bc13 enables a somewhat continuous range. In contrast, only a few temperature variables (bc5 and bc8) contribute to the Chaco gap. Temperature variables are more related to range restrictions in the North and the East. The northernmost boundaries in Brazil, where the range meets the Cerrado and is limited by high temperatures, are fairly well shaped by bc1, bc4, bc6, bc9, and bc11. As noted above, the modeled range

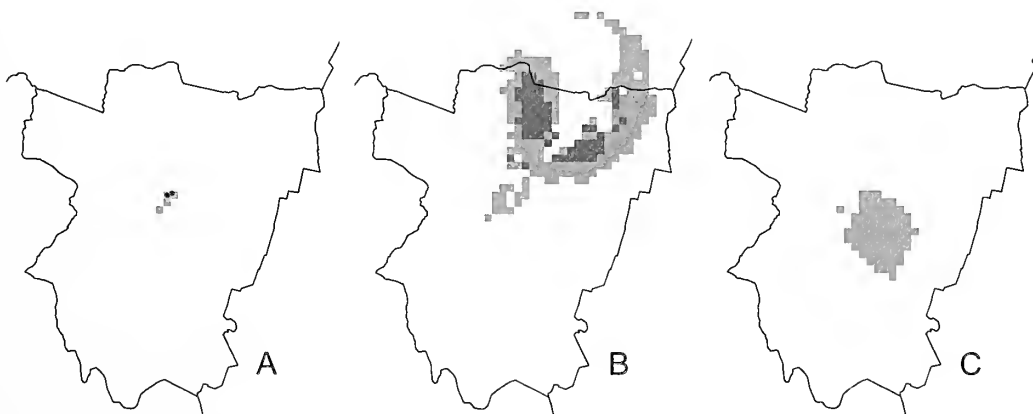


Figure 4.—Detail of the predictive modeling in province of Tucumán, Argentina. A: model with all 19 bioclimatic variables (small dots indicate the occurrence records), B: model with only temperature variables (bc1–bc11), C: model with only precipitation variables (bc12–bc19). Light grey: 0–25 percentile; dark grey: above 0.25.

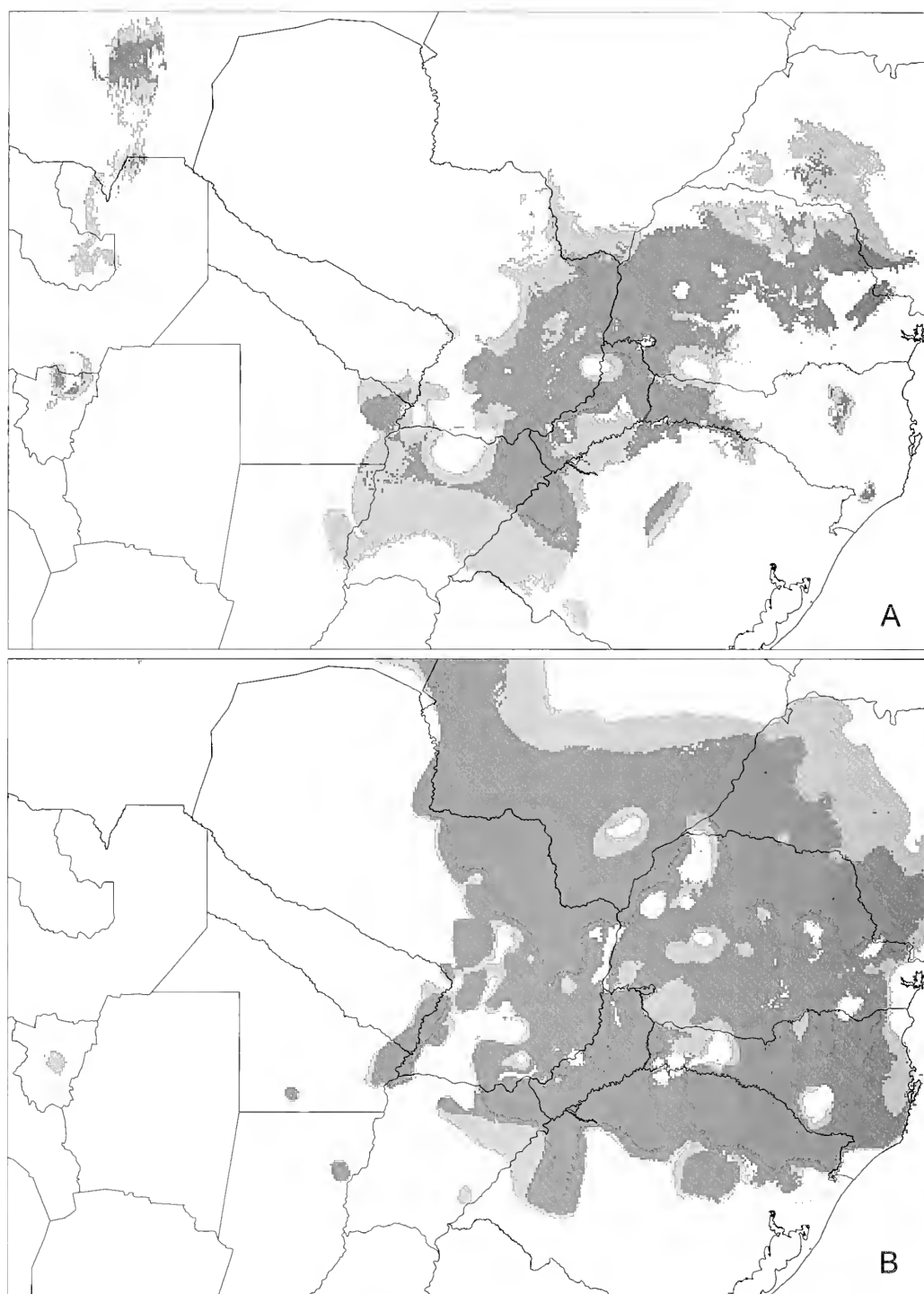


Figure 5.—Potential distribution of *Geraecormobius sylvanum* modeled only with temperature or precipitation variables (light grey: 0–25 percentile; dark grey: above 0.25). A: modeled range with temperature variables (bc1–bc11), B: modeled range with precipitation variables (bc12–bc19).

seems to circumvent the *Araucaria* forest, entering this ecoregion only marginally (Fig. 3). Several temperature variables (bc1, bc5, bc6, bc8, bc9, bc10, bc11) leave a defined gap there. The unsuitability appears to be related to the high elevation, which in turn causes the seemingly unsuitable cold climate: Clevelândia, elev. 890 m, is the highest record of *G. sylvanum* in Brazil and bears several extreme cold climate values (Table 2), but many negative sites in the *Araucaria* area are above 1100 m.

Accuracy.—Modeling with the training samples (30% of the original points randomly removed) consistently recovered the main portions of the range predicted with all points. More than half of the 20 repetitions matched in most parts of the core area, and just marginal sectors overlapped in only 10 repetitions or less. AUC values ranged from 0.8505 to 0.9402 (mean = 0.8935), and max- κ from 0.7082 to 0.8832 (mean = 0.7900); thus, individual and average AUC and max- κ values resulted in good to high model performances. These values are consistent

with performances of BIOCLIM obtained by Hernández et al. (2006) for similar sample sizes, and with comparative evaluations made by Sangermano & Eastman (2007).

DISCUSSION

As stressed by Peterson (2006), for the vast majority of species nothing more is known than a few “dots on maps” – and certainly, this applies for most Neotropical harvestmen, too. Ecological niche (or habitat suitability) modeling offers a first step towards inferring the basic ecological dimensions that are relevant to limit the species’ distribution. While previous knowledge just imprecisely related *G. sylvarum* to Paranense forests (and thereby assumed it was dependent on humid conditions), the bioclimatic analysis provided, for the first time, defined values to describe and discuss the species profile. The envelope method proved to be well suited as an initial approach when species records and biological knowledge are still scarce (Pearce & Boyce 2006). Results were convincing when matching the predicted range polygon to the Paranense forests ecoregion (Fig. 3), a biogeographical area that was previously associated with *G. sylvarum* based on a “non analytical, expert-based” assessment (Acosta et al. 2007). The model accuracy as measured by AUC and max-k was acceptable as well.

One of the main issues tackled in this paper, the Mesopotamia-yungas disjunction, received support from this model; but at the same time, some new questions arose concerning the presence of *G. sylvarum* in NWA. Despite the availability of presence records, the species is only weakly predicted there. This contrasts with other Mesopotamian harvestmen (*D. dilatatus* and *D. prospicius* among them) that, in preliminary models, were predicted in the yungas, with or without positive records in NWA (Acosta 2007). Both *D. dilatatus* and *D. prospicius* belong to the Mesopotamian *sensu stricto* sub-area (Acosta 2002), so their climatic requirements are not expected to be as humidity-dependent as for *G. sylvarum*. Since BIOCLIM is deemed to over-predict a species’ range (Peterson 2001), these facts, together with the profile values for some variables, suggest an important disparity of the bioclimatic conditions of NW and NE Argentina concerning preferences of *G. sylvarum*. However, one should not lose sight of the importance of the resolution of the climatic data. In general the resolution used (2.5 min) is acceptable at a regional scale, but its coarseness may not adequately reflect small-distance variations in montane areas, like in Tucumán (records range from 500 to 1250 m elevation within a distance of less than 3 km; i.e., less than the gridcell size).

As for the causes of the disjunction, a satisfactory explanation remains an open question. Acosta (1995, 2002) suggested that the disjunct ranges of the two *Discocyrtus* species may be a consequence of paleoclimatic cycles, with associated expansion/retraction events affecting the humid forests. A hypothetical vegetational “bridge” (as proposed by Nore 1992 for birds) would have acted as a corridor, enabling Mesopotamian harvestmen to expand their ranges up to the yungas, to leave isolated populations there as climate turned rigorous and the forests retracted. In the case of *G. sylvarum*, however, several elements may render this explanation less likely. Records in the yungas are actually few, indicating a

quite limited distribution, and the bioclimatic model accordingly predicts this species only weakly for the region. The yungas is one of the best sampled areas in Argentina for harvestmen (Acosta 2002), so it seems unlikely to find *G. sylvarum* elsewhere in NWA. People from the species’ core range are in general aware of *G. sylvarum*, probably because of its large size, abundance and strong odor. These conspicuous and smelly harvestmen are also locally well known in El Corte, although people that have lived there for the last 30 years suggest that the species “appeared” only in recent years (A. M. Frías, pers. comm.). These observations, together with the apparent tolerance of *G. sylvarum* to disturbed areas (Acosta et al. 2007), may suggest that transportation by humans in historic times might best account for the presence of this Mesopotamian harvestman in Tucumán.

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Ecology and web allometry of *Clitaetra irenae*, an arboricolous African orb-weaving spider (Araneae, Araneoidea, Nephilidae)

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Abstract. Analysis of ecological data of the arboricolous nephilid spider *Clitaetra irenae* Kuntner 2006, endemic to Maputaland forests, South Africa, indicates the species' dependence on this highly threatened habitat. We tested *C. irenae* habitat dependence via GIS analysis by plotting the known distribution against southern African ecoregions. In the southern part of its range, *C. irenae* inhabits almost exclusively one ecoregion, the Maputaland coastal plain forests; but further north, in tropical southern Africa, it continues inland into Malawi's woodlands. We test and refute the hypotheses that *C. irenae* inhabits exclusively mature trees, trees of a particular species, trees with a smooth bark, tree habitats at certain height above ground, and only closed canopy forest stands. The ecological niche of *C. irenae* is flexible as long as suitable trees under at least partially closed canopy are available. We quantify the *C. irenae* ontogenetic web changes from orb to ladder and the simultaneous hub displacement towards the top frame. Such web allometry allows the web to increase vertically but not horizontally, which enables the spider to remain on the same tree throughout its development and thus the ladder web architecture is an adaptation to an arboricolous life style. Adult hub displacement, common in spiders with vertical webs, is explained by gravity. *Clitaetra irenae* web orientation on trees correlates with forest closure, and might indicate the Maputaland forest quality. We argue for utilization of the ecology of arboricolous nephilid orb-weaving spiders (*Clitaetra* and *Heremnia*) in systematic conservation assessments in the Old World tropics.

Keywords: Behavioral ecology, evolution, conservation, Maputaland, South Africa, *Heremnia*

Opsomming. Analise van ekologiese data van die boombewonende nephilid spinnekop *Clitaetra irenae* Kuntner 2006, endemies tot Maputaland woude in Suid-Afrika, dui die spesie se afhanklikheid van hierdie hoogs bedreigde habitat aan. Ons het *C. irenae* habitat afhanklikheid via GIS analiese getoets deur die bekende verspreiding teen die suider-Afrikaanse ekologiese streke aan te teken. In die suidelike deel van die verspreiding kom *C. irenae* in slegs een ekostreek, die Maputaland kusvlakte woude, voor, maar verder noord in die verspreiding kom dit verder in die binneland, in Malawiese bosveld, voor. Ons toets en verwerp die hipotesisse dat *C. irenae* slegs volgroeide bome bewoon, bome van 'n spesifieke spesie, bome met gladde bas, boomhabitate op 'n sekere hoogte van die grond af, en slegs toe kroonbedekking woude. Die ekologiese nis van *C. irenae* is aanpasbaar solank daar geskikte bome onder ten minste gedeeltelike toe kroonbedekking beskikbaar is. Ons kwantifiseer *C. irenae* ontogenetiese webveranderings van 'n wawiel- na 'n leerweb en die gelyktydige verskuiwing van die kern na die bokant van die raam. Sulke web allometrie gee die spinnekop die vermoë om die web vertikaal te vergroot sonder horisontale veranderings, wat die spinnekop in staat stel om op dieselfde boom te bly regdeur sy ontwikkeling. Ons sien die leerweb dus as 'n aanpassing tot boomlewende gewoontes. Volwasse kern verskuiwing, algemeen in spinnekoppe met vertikale webbe, word deur gravitasie verduidelik. *C. irenae* se web oriëntasie op bome korreleer met kroonbedekking, en kan 'n aanduider wees van Maputaland woud kwaliteit. Ons stel voor dat nephilid wawiel-web spinnekoppe (*Clitaetra* en *Heremnia*) se ekologie gebruik word in sistematiese bewarings assesserings in die Ou Wêreld tropiese gebiede.

Identifying areas of high conservation value (systematic conservation assessment sensu Knight et al. 2006) is one of the main priorities of modern ecology and conservation biology. Traditionally, conservation assessments have been largely based on vertebrate biodiversity data, while data on more diverse groups such as arthropods remain poorly utilized. This is particularly true for species-rich tropical faunas, where the natural history and ecology of most arthropod species continue to be unstudied. Among spiders, a clade with nearly 40,000 described species (Platnick 2007) and many more projected (Coddington & Levi 1991; Coddington 2005), potential indicator species are rarely identified. Most recent studies have investigated the impacts of pollution, disturbance,

and habitat classification on spiders at the community level, while species-level studies have focused on effects on predation ecology and heavy metal assimilation (Marc et al. 1999). However, these studies primarily dealt with the European and American faunas, while examples from the Afrotropical region are unknown. Here, we investigate the ecology of the recently described *Clitaetra irenae* Kuntner 2006, an arboricolous nephilid spider endemic to southern African forests, and use the newly acquired behavioral and ecological data to test its dependence on a highly threatened habitat – the Maputaland coastal plain forests.

Maputaland is an ecological-geographical entity comprising the coastal plain of north-eastern parts of KwaZulu-Natal (South Africa) from Richards Bay (28°48'S, 32°05'E) in the south to Xai-Xai in southern Mozambique (25°02'S, 34°25'E)

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in the north, and extending inland along the Lebombo Mountain range into eastern Swaziland (Olson et al. 2001; Van Wyk & Smith 2001). Due to the high levels of plant and vertebrate endemism (Van Wyk 1994, 1996; Van Wyk & Smith 2001) and the patchy distribution of unique habitats such as sand forest, Maputaland is of prime conservation importance. Furthermore, the composition of certain faunal and floral assemblages of different sand forest patches are significantly different (e.g., Kirkwood & Midgley 1999; Matthews et al. 1999, 2001; Van Rensburg et al. 1999, 2000), which supports the conservation of this particular habitat and its accompanying biological diversity throughout the region. Maputaland appears among six out of nine global biodiversity conservation priority areas (Brooks et al. 2006), being recovered within the crisis ecoregions, the biodiversity hot spots, the endemic bird areas, the centers of plant diversity, and the global 200 ecoregions, as well as within a megadiverse country, South Africa (for details see Brooks et al. 2006, and references therein).

The Old World tropical nephilid spider genus *Clitaetra* Simon 1889 is important in araneoid systematics because of its phylogenetic position as the sister taxon to all other nephilids (Kuntner 2005, 2006); these, in turn, appear to be the basal araneoid lineage (Kuntner et al. 2008). While the large-bodied nephilids (*Nephila*, *Nephilengys*) are well studied (Kuntner 2007) and recognized as ecologically important in most (sub)tropical ecosystems, *Clitaetra* ecology has largely been unknown (but, see Kuntner 2006). Of the six known *Clitaetra* species only *C. irenae* (Fig. 1) biology has been studied in some detail—Kuntner (2006) focused on its web-building behavior and general natural history. *Clitaetra irenae* was found in South Africa's subtropical coastal dune and sand forests of northern KwaZulu-Natal, with an outlying museum record from Malawi (Kuntner 2006: fig. 26). As in the Australasian nephilid spider genus *Herennia* Thorell 1877 (see Kuntner 2005), *Clitaetra* species are obligate tree dwellers building orb-webs against tree bark (Figs. 1, 2), with a few centimeters clearance between the planar web and the substrate. As in *Herennia* (Kuntner 2005), *Nephilengys* Koch 1872 (Japyassu & Ades 1998; Kuntner 2007), and *Nephila* Leach 1815 (Bleher 2000), juvenile *Clitaetra* webs resemble standard araneoid orb-webs (Figs. 2D, E). However, the webs of adult female *C. irenae* are highly modified *ladder webs* (Figs. 2A, C), defined as two dimensional orb-webs with parallel side frames and zig-zag sticky lines substituted for spirals (Kuntner et al. 2008:fig. 23). The species' apparent dependence on a particular habitat (Maputaland forests) and microhabitat (mature trees), as indicated by historical distribution records and the distribution of these particular forests, prompted our detailed investigation into its behavioral ecology emphasizing its ontogenetic web architecture shifts.

We investigate *C. irenae* web allometry by quantifying the developmental modification of the orb web into a ladder, pose a behavioral explanation for such an allometric shift, and deduce its ecological implications. Through explicit hypotheses (below) we examined whether or not the web modification in *C. irenae* correlates with a particular habitat type, with climatic conditions and/or altitude, and whether the species depends on mature Maputaland forests for sustainable populations. A species that is a narrow endemic of southern

Africa and a narrow habitat specialist (an obligate tree dweller) in a threatened coastal plain habitat is potentially at risk of habitat loss, and could be added to the list of species used as indicators of habitat quality.

Specifically, we tested the following hypotheses:

- (1) *Endemism*: Kuntner (2006) suggested that *C. irenae* was endemic to northern KwaZulu-Natal. However, such an hypothesis was defined geographically, not ecologically, and failed to explain the single outlying record from Malawi (Kuntner 2006). We tested whether *C. irenae* is endemic to the wider Maputaland (including Mozambique and Swaziland) by using precisely defined ecoregions (Olson et al. 2001).
- (2) *Habitat preference*: Most material examined by Kuntner (2006) was collected in sand forests along the Maputaland coastal plain. We investigated Kuntner's (2006) expectation that *C. irenae* is confined to mature sand forests. During our survey we noted the habitat type and canopy closure.
- (3) *Tree preference*: To test the spiders' dependence on a particular tree species we attempted to identify all trees where spiders were found. We predicted the spiders would prefer a particular tree species as vaguely suggested by Kuntner (2006).
- (4) *Tree size*: If the species was confined to mature forests, we predicted that larger spiders would prefer larger trees, and that web size would correlate with spider size.
- (5) *Substrate (bark) structure*: To test if the spiders utilize certain types of substrate, we classified bark into three categories (smooth, medium, or rough). We expected that trees with smooth bark would be more likely to host these spiders as the uneven surface of rough bark may hinder two-dimensional web construction.
- (6) *Website orientation*: The spider's website orientation on a tree might differ between closed canopy forests and partially open canopy tree stands (woodland/thicket) due to sunlight penetration. Assuming that the species is indeed native to closed canopy forests and that inhabiting other types of tree stands is an artifact of habitat fragmentation, we expected that we would find no web orientation preference in closed canopy stands, where continuous direct sunlight is an exception. In contrast, in more open tree stands where webs could potentially be exposed to direct sunlight, web orientation should be away from the sun (to the south).
- (7) *Distance from ground*: Finally, we tested for differences in web height above ground among the spider instars (size classes). We predicted that spiders would preferentially occupy lower positions on a tree as they age because larger tree trunk circumference closer to the ground would be more suitable for larger webs.

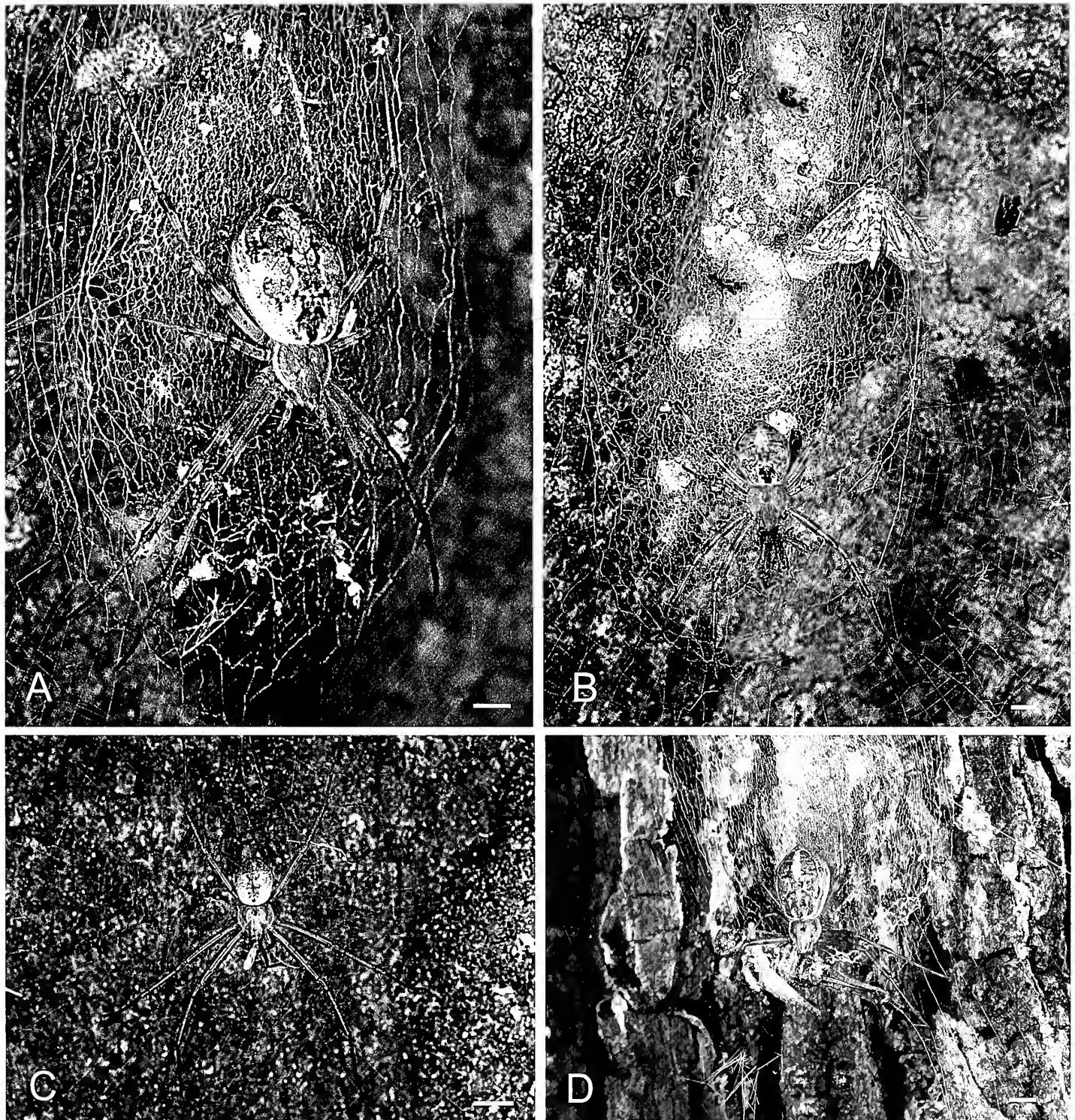


Figure 1.—*Clitaetra irenae* from South Africa (A–C, Fannies Island, 2001; D, Ndumo Game Reserve, 2006): A. Female holotype (see Kuntner 2006) at the hub of her web; B. Female feeding at the hub of her web; note the egg-cases above the hub camouflaged with prey remains; a male was present in her web (not shown); C. Paratype male (see Kuntner 2006) at the hub of his orb web, feeding on dipteran prey; D. Subadult female at web hub, feeding on cricket. Scale bars = 1.0 mm.

- (8) *Web allometry*: *Clitaetra irenae* web architecture shifts during spider ontogeny from orb to ladder web. Thus, we predicted that the *ladder index* and the *hub displacement index* (both defined below) would increase with spider size.

METHODS

Field study.—We visited six reserves (Fig. 3) in KwaZulu-Natal (South Africa) between 9–30 April 2006, the period when adult *Clitaetra irenae* are known to occur (Kuntner 2006). These reserves (Ndumo Game Reserve, Tembe Ele-

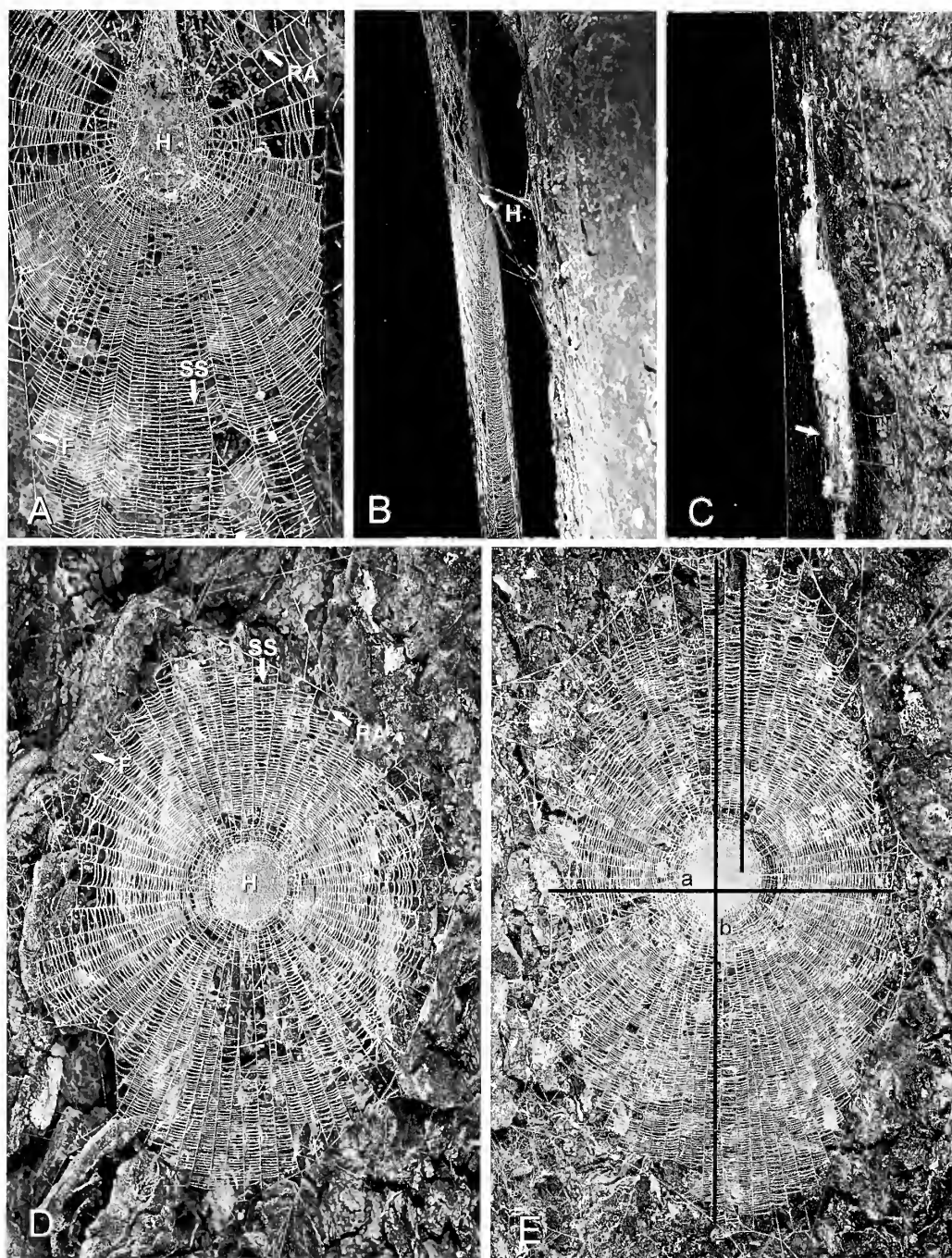


Figure 2.—*Clitaetra irenae* web architecture: A–C. Adult female webs: A. Frontal view, note ladder shape of web with parallel side frames (F), “sticky spiral” (SS) not spiralling, with silk enforced hub (H) displaced towards top frame; B. same web, lateral view; C. Female (arrow) in web, with first instar offspring in upper web; above hub is empty egg sac. D. Juvenile web (second instar); note typical orb-web architecture with bent side frames (F), round sticky spiral (SS), and upper radii as long as lower ones. E. Another second instar web, with parameters measured (a = web width, b = web height, c = top frame to hub). Photographs by M. Kuntner taken in Ndumo Game Reserve, South Africa, 2006; web measurements (cm) in A, B: a = 8, b = 29, c = 10.5; D: a = 5, b = 11, c = 5.5.

phant Park, Kosi Bay Nature Reserve, Sodwana Bay National Park, Hluhluwe-Imfolozi National Park, and the Greater St. Lucia Wetlands Park) slightly surpass the previously known *C. irenae* geographic range, except for the Malawi datum (Kuntner 2006), and therefore test the species’ geographical limits in Maputaland. Within the reserves we searched for the easily recognizable species (females, see Fig. 1A; males, see

Fig. 1C; for identification details see Kuntner 2006) at various localities, focusing on all available habitat types.

Where more than a single *C. irenae* spider was found, we measured the following ecological and behavioral parameters on all webs: date of collection; locality; site; habitat; latitude and longitude; host tree species (if known); tree bark structure categorized as smooth (as exemplified by *Celtis africana*),

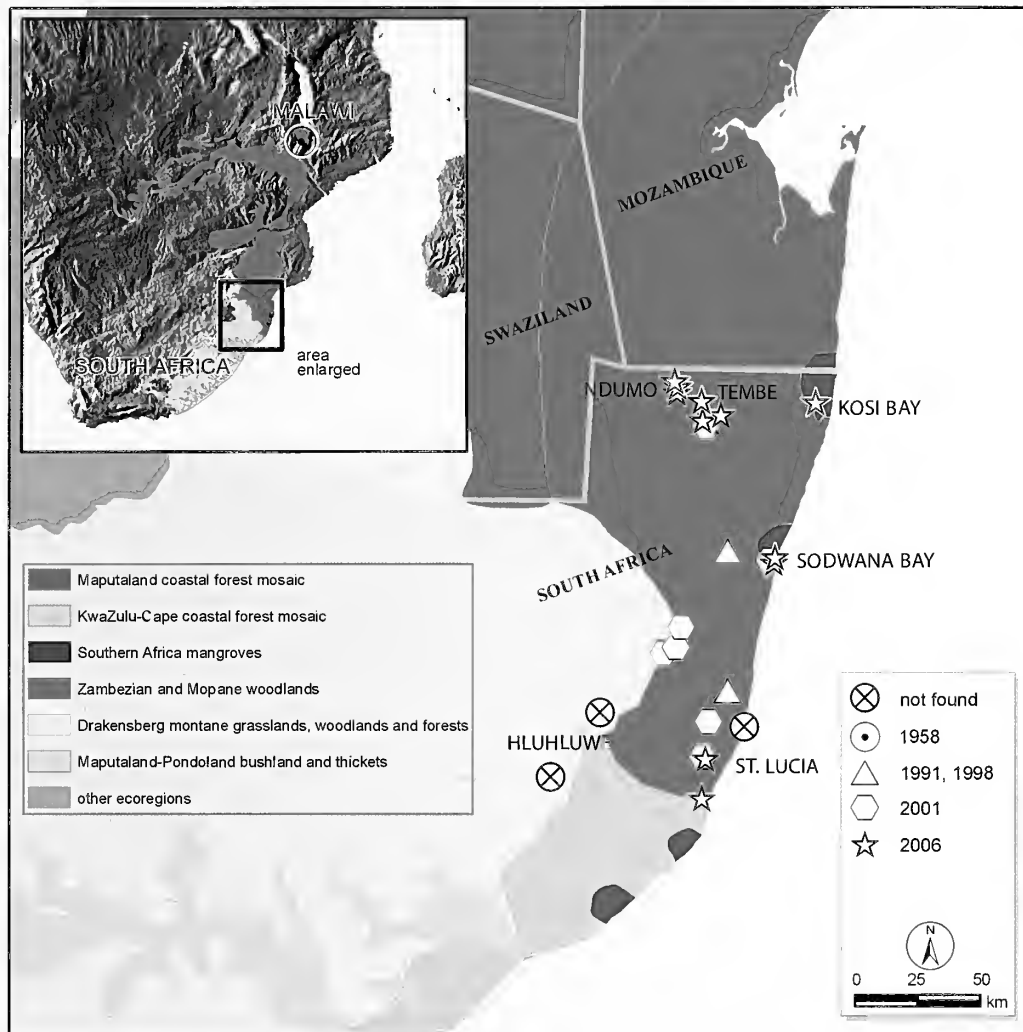


Figure 3.—*Clitaetra irenae*, currently known distribution plotted against southern African ecoregions. The outlying 1958 Malawi record (see Kuntner 2006) falls into “Zambezian and Mopane woodlands,” which stretches south adjacent to “Maputaland coastal forest,” the species’ prime ecoregion. The 1991–2001 data are from Kuntner (2006), new field records (2006) are from this study.

medium (as in *Balanites maughamii*), or rough (as in *Acacia nigrescens*); tree trunk circumference at the level of spider web hubs; canopy coverage categorized as closed, partially open, or open; stage or instar number; web width (Fig. 2E), web height (Fig. 2E), distance from web hub to top frame (Figs. 2D, E) and web hub height above ground; website orientation (8 directions: N, NE, E, SE, etc.), and possible further comments.

The first six (autecological) parameters document locality, habitat, and test hypothesis 2 (habitat preference). The next four parameters, i.e., host tree species, bark structure, trunk circumference and canopy coverage, are microhabitat data and test hypotheses 2–5. Spiders were assigned to seven categorical size classes (stages) corresponding to ontogenetic instar numbers (size correlates with age and instar number). Instar numbers were estimated from relative spider size, falling into fairly discrete size classes, assuming seven post-egg sac instars during female ontogeny: adult females were scored as 7, newly hatched animals 1, and others fell in between up to 6

(penultimate). Instars 2–7 build their own webs, but first instar spiderlings remain in the mother’s web (Fig. 2C). No developmental study has been done on *Clitaetra*. The assumption of seven instars in *C. irenae* ontogeny follows from data on other nephilids; e.g., the giant females *Neplila pilipes* (Fabricius 1793) go through about 10 juvenile instars while the small males go through about 4, the number of molts depending on the season and food availability (Higgins 2002). Three web parameters, namely web width, web height, and distance from hub to top frame, quantified developmental shifts in webs (see below). The last two parameters, distance from hub to ground and website orientation, indicate microhabitat preference and test hypotheses 6 and 7.

In order to increase visual contrast, webs were dusted with cornstarch for measurement and photography. All measurements were taken with a tape measure and are reported in centimeters, unless noted otherwise. Web orientation was taken with a compass. Web architecture abbreviations are: H = hub (Figs. 2A, B, D, E); F = frame (Figs. 2A, D); RA =

radius (Figs. 2A, D); SS = sticky spiral (Figs. 2A, D); a = web width (Fig. 2E); b = web height (Fig. 2E); c = upper web height = distance top frame to hub (Fig. 2E).

Web allometry.—We derived two ratios quantifying web allometry. The *ladder index* is the relative web height, defined as the ratio of web height to web width, and quantifies the transition from orb to ladder web during ontogeny. Similar to web shape sensu Zschokke (1993), the ladder index, as used here, differs in values increasing with extreme architecture. *Hub displacement* is lower orb/total web height using the formula $(b-c)/b$, where b = web height and c = top to hub (Fig. 2E). Hub displacement index is similar to web asymmetry indices of Masters & Moffat (1983), Rhisiart & Vollrath (1994), and Kuntner et al. (2008), but its values increase rather than decrease with the hub being eccentric towards the top web frame.

Statistical analyses.—We explored the relationships between the spider size (instar) and the following variables: 1) web height, 2) web width, 3) distance of web from the ground, 4) tree circumference, 5) ladder index, and 6) hub displacement index. Web parameters were plotted as box-plots (Tukey 1977). Due to the low number of webs in stages 4 and 5, individual points were plotted for these stages. Differences in medians between stages 2 and 7 were tested using the Mann-Whitney *U*-test. Freely available statistical environment R (R Development Core Team 2006) was used for plotting and for significance tests. Web orientation on trees (eight main directions) was interpreted through circular statistics using the Rayleigh test (Fisher 1993).

GIS analysis.—In order to test hypothesis 1 (endemism), we analyzed all available *C. irenae* locality data (Kuntner 2006; this study) using GIS. Our analysis builds on the digital base map by Bletter et al. (2004), which was obtained from the New York Botanical Garden (http://www.nybg.org/bsci/digital_maps/), with permission from the authors. The base map, which derives from the Environmental Systems Research Institute (ESRI) data sets ArcWorld®, ArcAtlas®, and Digital Chart of the World® (<http://www.esri.com/>), was built specifically for the Neotropics (Bletter et al. 2004), but also contains detailed data on the World's terrestrial ecoregions (Olson et al. 2001), courtesy of the World Wildlife Fund (<http://www.wwf.org/>). Olson et al. (2001) recognize 867 terrestrial ecoregions worldwide, which is a much improved resolution compared with previous attempts to classify terrestrial biotas. The map delimits six ecoregions within the geographical limits relevant to this study (Fig. 3). The *C. irenae* locality data (1958; 1991–2001 data are from Kuntner (2006); new field records (2006) are from this study) were superimposed on the southern African part of the base map using ArcView® GIS.

RESULTS

Clitaetra irenae occurred in all reserves (Fig. 3) except Hluhluwe-Imfolozi National Park, which falls into the Drakensberg montane grasslands, woodlands, and forests ecoregion (Fig. 3). In Kosi Bay and Sodwana Bay the spiders were present but their abundances per trees were too low to be measured. In some reserves, e.g., Ndumo and Tembe, the species was abundant. The outlying record of a single *C. irenae* male from Malawi (1958 datum from Kuntner 2006) falls on

the ecoregion “Zambezian and Mopane woodlands,” which stretches south adjacent to “Maputaland coastal forest” (Fig. 3), the species' main ecoregion.

Figure 4 summarizes the data obtained in Ndumo Game Reserve, Tembe Elephant Park and the two localities in the Greater St. Lucia Wetlands Park. The full data set with exact geographical coordinates for each habitat within the reserves is published online at www.nephilidae.com. In total, we investigated 166 spiders and their webs, the majority ($N = 118$, 71%) being second instars; the numbers of other instars investigated were much lower (Fig. 4A). Habitat preference characterizes the four forest types where the webs were measured (Fig. 4B). We characterized the habitat at Nyamiti Hide (Ndumo Game Reserve), where the majority of the aggregated second instar webs were found, as “riverine bush” (“deciduous orthophyll scrub with trees” of De Moor et al. (1977); “subtropical bush” of Haddad et al. (2006)), since the tree stands had a partially open canopy, with the terrain sloping gradually towards the Nyamiti Pan. Fig. 4C show that the most data (133 individuals) were taken in forest stands with only partially open canopy (riverine bush at Nyamiti Hide was all partially open habitat), and that all sand forest patches examined (Ndumo, Tembe, St. Lucia) were closed canopy (33 data points). There was little overlap of tree species (if known) between localities. However, sand forest trees harboring spider webs had a smooth and medium bark texture, while those in riverine bush had rough or medium bark (Fig. 4D).

Figures 5A–F show the relationships of interval and ratio data by instar, and report the results of the non-parametric comparisons (Mann-Whitney *U* test) of instar 2 ($n = 118$) and 7 ($n = 18$). Web height and web width increased significantly with spider size (Figs. 5A, B, $P < 0.001$). These two relationships support our assumption that spider web size correlates with age (instar). No significant differences were found in the web distance from the ground (Fig. 5C, $P = 0.39$) among the spiders of different size. Contrary to our prediction, larger spiders did not prefer larger trees (Fig. 5D, $P = 0.15$). However, as predicted, both measures of web allometry, i.e., the ladder index (Fig. 5E, $P < 0.001$) and the hub displacement index (Fig. 5F, $P < 0.001$), increased with spider size.

Figure 6 plots web orientation frequencies in eight categories (north, northeast, east, etc.) using circular statistics (Fisher 1993). Pooling all data (Fig. 6A) shows that *C. irenae* webs were randomly distributed on all sides of trees. However, the closed canopy data (Fig. 6B) reveal a significant (Rayleigh test, $P < 0.05$) preference for the northern side of trees, and the partially open canopy data (Fig. 6C) plots as significantly bimodal (Rayleigh test, $P < 0.05$), the spiders preferring southern and eastern faces of trees. Similarly, we found that the webs on smooth bark (only found in closed canopy sand forests), showed a significant preference towards the north. However, the webs on medium bark (closed and partially open forests), and on rough bark (only in partially open canopy forest), showed random distributions. The northern orientation of webs under closed canopy is related to canopy closure, not bark type, as both subsets of webs, the smooth bark webs and medium bark webs showed a significant preference for the northern side of trees (Rayleigh test, $P < 0.05$ and $P < 0.1$, respectively).

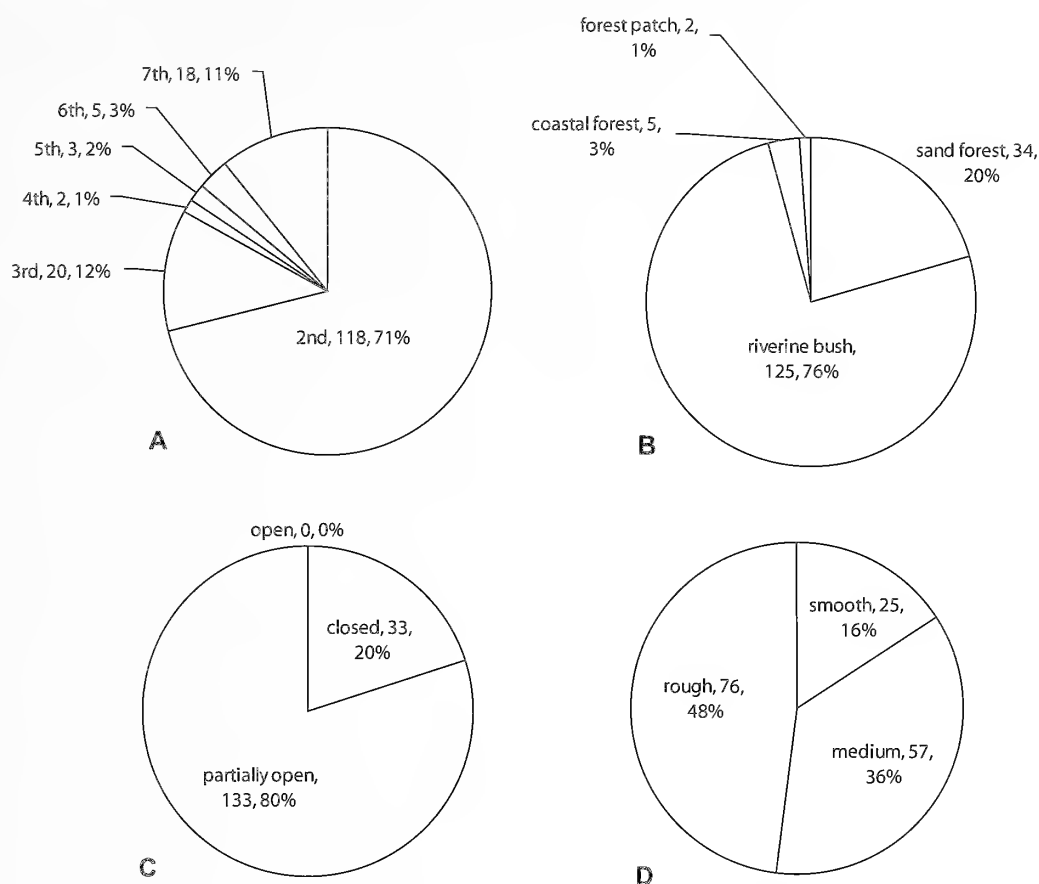


Figure 4.—Field data summary (category, *n*, percentage): A. Individuals by instar; B. Habitat; C. Canopy coverage; D. Bark structure.

DISCUSSION

The disproportionately high numbers of small juveniles (instar 2) measured compared to other instars (Fig. 4A) may be explained by the fact that second instars tend to aggregate around the mother's web and are thus more easily located than instars 3–6. One of the alternative explanations, the higher mortality of larger juveniles, is contradicted by the fact that 18 females versus fewer 4–6th instar juveniles were collected (Fig. 4A). Seasonality seems the best explanation: as our study focused on the known adult *C. irenae* phenology, our April field work only sampled a part of the species' life cycle.

Distribution and phenology.—The ecoregion with the majority of *C. irenae* records (Fig. 3) is the Maputaland coastal forest mosaic, but some records also fall into the adjacent ecoregions, including the Southern Africa mangroves and the KwaZulu-Cape coastal forest mosaic. The localities we visited that fall into these latter two ecoregions were no different with regards to forest structure and tree and bark microhabitat from the ones falling into Maputaland, and thus we view these records as continuous with "larger Maputaland." At this resolution, the borders between these ecoregions are fairly arbitrary. It should be noted, however, that two of the three South African localities visited where *C. irenae* was not found are "Drakensberg montane grasslands, woodlands and forests" (Fig. 3), whose forest microhabitat structure is quite different from Maputaland. These habitats are further inland and at higher altitudes than *C. irenae* typically inhabits, perhaps indicating particular microclimatic, altitudinal and

habitat preferences. We predict that in the south the species inhabits Maputaland coastal forests into Mozambique, but that further north in tropical southern Africa, it continues inland into the adjacent ecoregion (the Zambezian and Mopane woodlands) as far north as Malawi. Although no specimen records currently exist from Mozambique and Swaziland, we predict that the species occurs there. Our data support the endemism hypothesis by 1) showing the continuity of the Maputaland forest mosaic ecoregion into Mozambique, and by 2) showing the ecoregion Zambezian and Mopane woodlands' adjacency to Maputaland. Where found, the *C. irenae* adult abundances were greatest during the beginning of our study (11–13 April 2006) while towards the end (28–29 April 2006) no further adults were found.

Habitat preference.—No *C. irenae* webs were measured in open canopy stands (Fig. 4C), which is not to be interpreted to mean that the spiders never occur there. In Maputaland *C. irenae* inhabits most tree habitats, including lone trees in semi-open canopy areas, and even synanthropic vertical surfaces, but preferentially occupies partially open and closed canopy stands. However, three of the four habitats where spiders and their webs were investigated in detail are forests (Fig. 4B), which is consistent with our assumption that forests and not other types of tree stands are the species' prime habitat. Evidently, the species is not confined to sand forests, refuting our hypothesis 2. We also conclude that *C. irenae* does not exclusively inhabit closed canopy forests (Fig. 4C), and is much more common in partially open stands (see below).

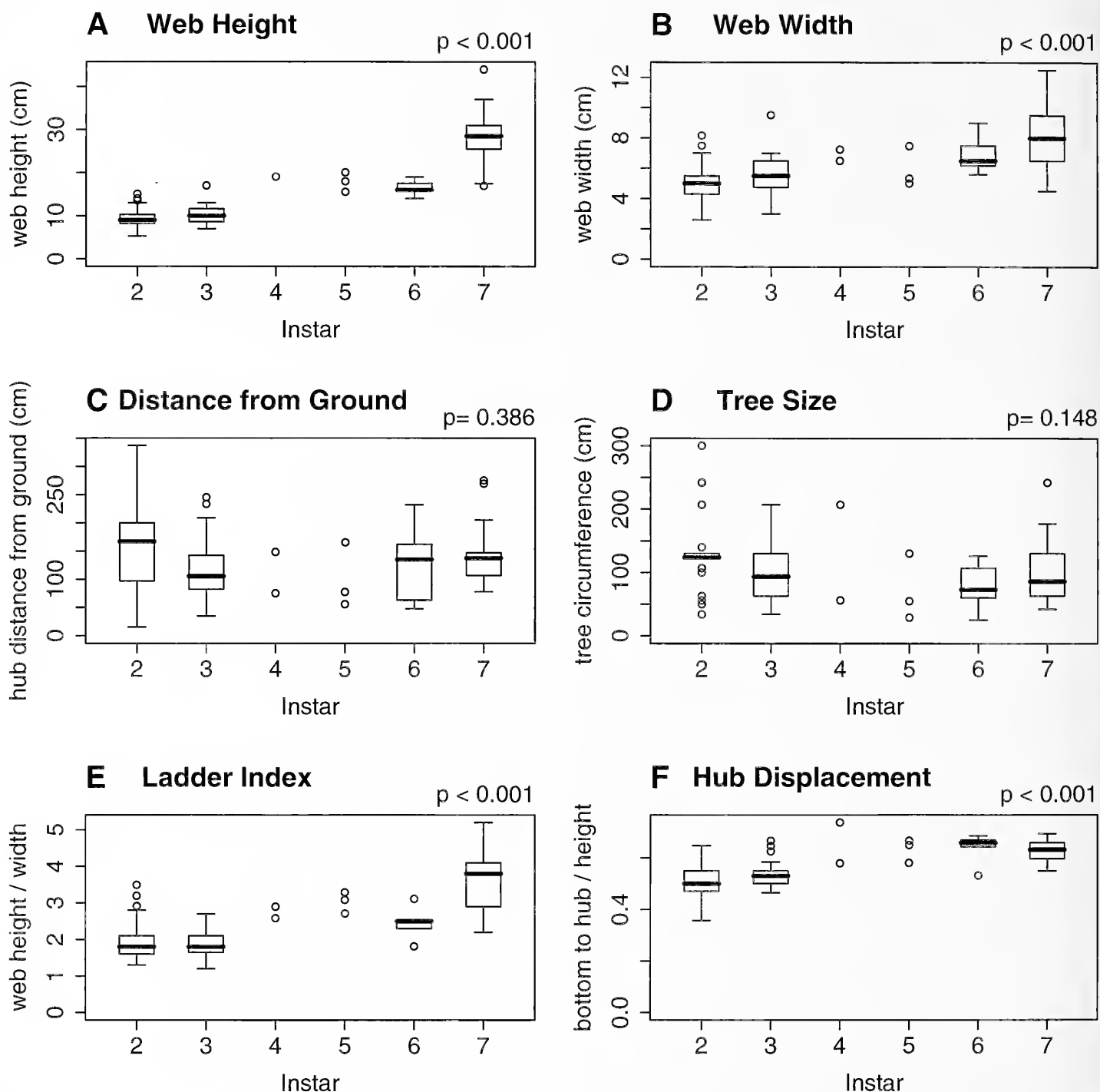


Figure 5.—*Clitaetra irenae* web parameters by spider size (instar number): A. Web height; B. Web width; C. Distance from ground; D. Tree size preference; E. Ladder index; F. Hub displacement. Differences between stages 2 and 7 were tested (Mann-Whitney U test), shown as P values.

Many trees with *C. irenae* webs ($n = 71$) could not be identified to species, but evidently *C. irenae* do not associate with one or a few particular tree taxa, nor with trees of a particular bark structure, refuting the hypotheses 3 and 5. This is reflected in the diverse habitats in which the species was encountered, each of which contains unique plant assemblages.

Our predictions that larger spiders chose larger, matured trees, and lower portions of trees, ignored web allometry and were based on the assumption that spider web size increases

with age. While the measured webs indeed increased with age (Figs. 5A, B) the fact that a variety of tree trunk sizes were utilized by each instar (Fig. 5D) refutes our hypothesis 4. Similarly, spiders of a certain age showed no preference for website height above ground (Fig. 5C) refuting the hypothesis 7. This would indicate a fair degree of tolerance to microclimatic variation with web height above ground (varying between 15.5 cm and 337.0 cm), which are expected to differ substantially from ground to canopy height. Dispersal of second instars and subsequent web construction

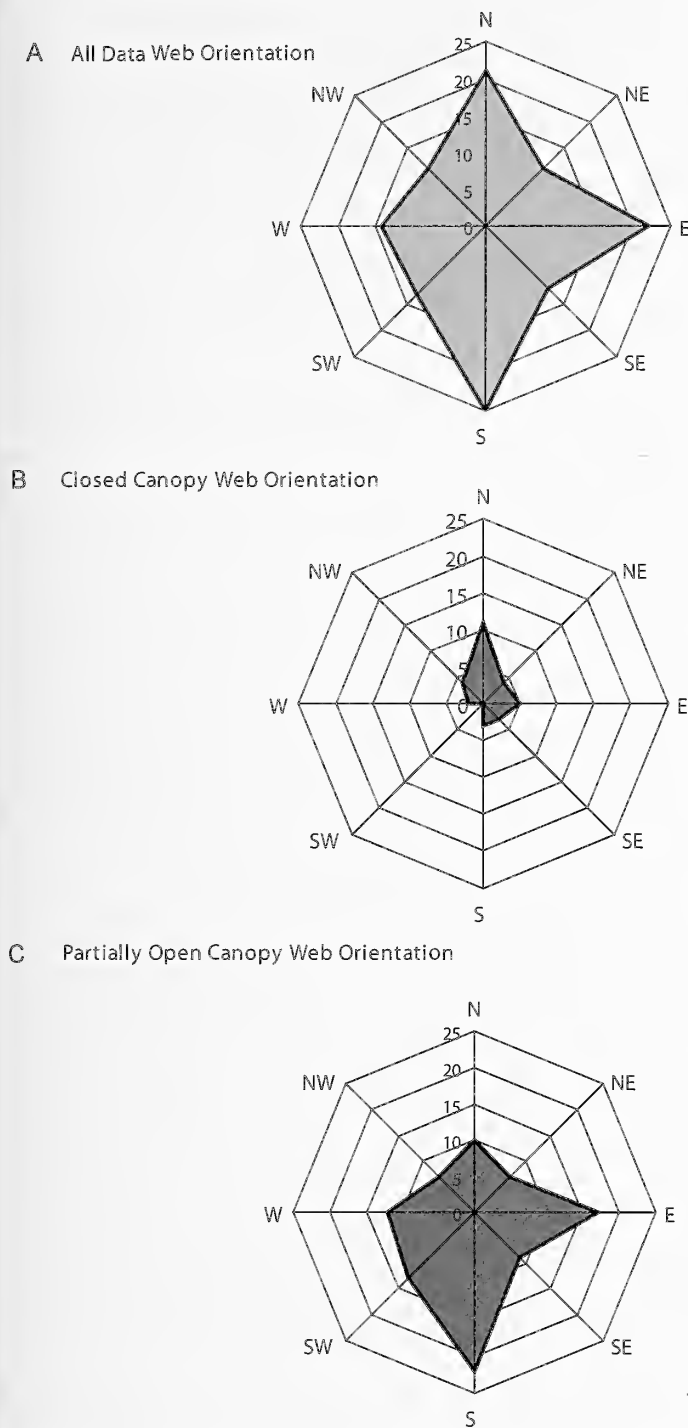


Figure 6.—*Clitaetra irenae* web orientation using circular statistics (Fisher 1993): A. All data (no orientation preference detected); B. Closed canopy forest (significantly north); C. Partially open canopy forest (significantly bimodal, south or east). Light versus dark grey graph colors represent statistically insignificant versus significant (Rayleigh test, $P < 0.05$) orientation.

appears to be in the immediate vicinity, and on the same tree, as the mother's web.

Web allometry.—The two indices quantifying the ontogenetic web changes from orb to ladder and the simultaneous hub displacement towards the top frame (Figs. 5E, F) both increase with spider size, which supports the prediction of

hypothesis 8. Such web allometry explains the lack of correlation between spider age and tree size. The ladder index, which is the relative web height, increases significantly with age, which is consistent with our initial observations of modified adult webs (Fig. 2). To a growing spider and its web the limiting factor on a tree of a given size is the horizontal website availability (tree circumference). The observed ontogenetic web allometry allows the growing spider's web to increase vertically, while at the same time the corresponding horizontal web increase is not required, allowing the spider to remain on the same tree. The smallest tree on which an adult female web was constructed (tree circumference 42.0 cm, web width 6.5 cm) would suggest that the curvature of the tree trunk may also play a role in the web site selection, making available points of attachment on the bottom and top of the web but eliminating the restriction of horizontal attachment points on the side of the web. We see the ladder web as an adaptation to an arboricolous life style because it eliminates the need of a potentially costly and dangerous walk from one (smaller) tree to another (larger) tree. Ants, which are abundant on trees where *C. irenae* occur, may be important predators (Kuntner 2006). However, ants are not known to invade webs. Thus, orb-web spiders may be safer from predators on (or close to) their webs than walking about.

The webs of all adult nephilid spiders have displaced hubs, mostly towards the top (for rare horizontal displacement in *Nephilengys*, see Kuntner 2007). Hubs are often displaced above the web center in other araneoid spiders with vertical webs (see Kuntner et al. 2008), notably in araneids. The logical explanation for an ontogenetic shift from a central hub in small juveniles towards the eccentricity seen in larger, heavier spiders is gravity. Masters & Moffat (1983) demonstrated that predation success of the araneid spider *Larinioides scolopetarius* (Clerck 1757) improves in webs with hubs displaced above the web center, as the time to reach the prey upwards and downwards is thus optimized.

Ladder webs on tree trunks, present in the extant species of the basal *Clitaetra-Herennia* grade, were the ancestral life style of the pan tropical clade Nephilidae and reversed to aerial orb webs in the ancestor of *Nephila* (Kuntner et al. 2008). All nephilids, *C. irenae* included, retain the non-sticky spiral (NSS) in their finished web unlike most other orbweavers (Kuntner 2006; Kuntner et al. 2008). NSS or auxiliary spiral functions as a guide during the spider's sticky spiral construction (Zschokke 1993). Unlike in *Nephila* and *Nephilengys*, NSS in *Clitaetra* webs is difficult to discern, perhaps because these spirals are thin and may get stuck with the narrowly meshed sticky ones. Kuntner (2006) determined the NSS presence by observing the spiders build at night (and not cutting the NSS when laying the sticky spiral), and the same could not be determined by photographs of finished webs. The retention of the NSS in nephilids has been suggested to have evolved in response to female gigantism (Hormiga et al. 1995). However, NSS seems to have been present in the nephilid ancestor, where sexual dimorphism was only moderate and not extreme (Kuntner et al. 2008). Perhaps the retention of NSS was originally related to ladder web architecture, and its presence in derived nephilids represents evolutionary time lag. The convergent presence of NSS in *Scoloderus* webs (below) may also be related to ladder web architecture.

While ladder web architecture is homologous in *Clitaetra* and *Heremnia* (Kuntner et al. 2008), it is clearly not related to, and differs functionally from, other known araneoid ladder webs. For example, neotropical *Scoloderus* builds an extreme ladder and, as in nephilids, retains the NSS (Eberhard 1975: fig. 2), but this web is aerial, not arboricolous, and its hub is displaced to the lower, not upper frame of the web, making the spirals above the hub resemble a ladder. The hub of the extreme ladder web of an unidentified araneoid from New Guinea described by Robinson & Robinson (1972), however, is displaced up as in nephilids, but that web is aerial and apparently lacks the NSS. Furthermore, while nephilid ladder webs are permanent structures (Kuntner 2005, 2006; Kuntner et al. 2008), the above webs are taken down daily and rebuilt every night (Robinson & Robinson 1972; Eberhard 1975). Ladder webs apparently evolved convergently in araneids and nephilids, perhaps in order to exploit new websites (trees) or food resources. The first may be particularly true for nephilids: while no study has focused on the prey of *Clitaetra* and *Heremnia* these spiders exploit tree trunks as websites and *Heremnia* even evolved a unique web design using *pseudoradii* (Kuntner 2005; Kuntner et al. 2008). Eberhard (1975) pointed out that a ladder web architecture allows for a more constant mesh size than any circular orbweb, which may be related to specialization for certain prey types. Aerial ladder webs have been suggested to represent convergent adaptation for ensnaring moths (Eberhard 1975; Stowe 1978). However, prey capture in tropical spiders is often anecdotal. While Stowe (1978) showed that 68% of 212 prey items of *Scoloderus* were moths, Robinson & Robinson (1972) observed a single prey item, a moth, attracted into the ladder web of their unknown spider by a light source. Although the focus of our study was not a quantification of *C. irenae* prey, the few sporadically observed insect prey items in their webs (Fig. 1A–D: Orthoptera, Diptera, Lepidoptera (Pyrilidae), Homoptera) suggest that the species is an opportunistic predator not particularly specialized on moths.

Web orientation.—Superficially, *C. irenae* webs appear randomly oriented (Fig. 6A). However, preferential spider web orientation occurs in both closed and partially open canopy forests. In closed canopy forests (Fig. 6B) the spiders show a preference for the northern side of the tree, refuting the first part of the web orientation hypothesis (that no orientation preference would be shown in closed canopy forests). Two types of bark that were found under closed canopy (smooth, medium) both show a significant orientation to the north, which indicates that northern orientation of webs under closed canopy is related to canopy closure, not bark type. Conversely, in partially open canopy forests (Fig. 6C) the spiders preferentially chose southern and eastern faces of trees, which is supportive of the second part of our hypothesis 6.

Web orientation probably affects web microclimate. Prolonged direct sun exposure could harm the spider or its web, or may affect prey availability and/or predation pressure. In the southern hemisphere, the predicted preference for the southern, shady side of trees makes sense in a partially open forest. It is somewhat surprising, however, that the spiders inhabiting closed canopy forests seem to prefer a northern (perhaps warmer) orientation, where we predicted randomness, though

this result does not, per se, refute hypothesis 6. Since we mainly scored smooth barked trees in sand forests (all closed canopy) it is not surprising that the web orientation patterns on smooth bark trees resemble those of closed canopy forests (Fig. 6B). The preference for the southern and eastern sides of trees in partially open canopy habitats (Fig. 6C) would suggest an aversion for direct sunlight and a preference for darker sides of trees.

Implications for Maputaland ecology.—Previous Maputaland studies have focused on organisms such as dung beetles and birds to assess community heterogeneity and the impacts of habitat destruction and regeneration on faunal and floral components (Van Rensburg et al. 1999, 2000; Davis et al. 2002; Wassenaar et al. 2005). However, Maputaland arachnids are highly diverse, with 457 species recorded from the Ndumo Game Reserve, 10,112-ha in size (Haddad et al. 2006). Given such diversity it is likely that several species are endemic to Maputaland and could be used as indicators of changes and disturbances to habitats, including sand forest.

Spiders are generally more sensitive than other arthropod groups to the vegetative structural conditions in a habitat, particularly web-builders (e.g., Marc et al. 1999; Stiles & Coyle 2001; Finch 2005). In monitoring or habitat evaluation using spiders as bio-indicators, the absence of species typical for a habitat (stenotypic species) is often indicative of low habitat quality, including vegetation structure (Bonte & Maelfait 2001). Thus, the identification of a sensitive species in the Maputaland fauna could provide an indication of the current condition of forest patches and the extent of disturbance to which the local fauna is presently being exposed. Once identified, indicator spider species can also be used for long-term monitoring of landscapes (Bonte et al. 2002), which will enable conservationists to assess changes in the condition of these forests over time. A particularly important current conservation issue in South Africa is the impact of heavy utilization of sand forests by elephants in the Tembe Elephant Park, Maputaland. This is thought to lead to the irreversible opening up of the sand forest into a structure comparable to mixed woodland (W.S. Matthews pers. comm.), which is likely to have a strongly negative long-term effect on the plant and animal communities, and on the diversity of the sand forest. Additionally, the growing rural human population in Maputaland is putting increasing pressure on sand forest patches outside conservancies (Kirkwood & Midgley 1999).

In Africa, particularly, forests are opened up by big game, and such forest gaps are not necessarily indicative of unnatural disturbance. Indeed, in the reserve where elephants occur (Tembe), partially open canopy patches seem to be continuous with closed canopy sand forests. Thus, our finding of most individuals of *C. irenae* in partially open canopy forest stands does not refute our hypothesis about *C. irenae* dependence on the undisturbed Maputaland forest habitats. This could be an artifact of our under-sampling of closed canopy locations. Assuming that indigenous, undisturbed Maputaland forests are closed canopy, and thus the original preference of *C. irenae* spiders in a quality habitat is towards the north, scoring web orientation might be indicative of forest quality/disturbance. The easy *C. irenae* identification (Fig. 1, see Kuntner 2006) warrants further investigation as to whether it might be a suitable bioindicator.

Conclusions.—The data at hand suggest the ecological and behavioral dependence of *C. irenae* on the threatened Maputaland forests. The wider Maputaland endemism hypothesis receives support, but the hypotheses that *C. irenae* inhabits exclusively sand forests, mature trees, trees of a particular species, trees with a smooth bark, tree habitats at certain height above ground, and only closed canopy forest stands, are refuted. Evidently the species' ecological niche is flexible to an extent but requires suitable tree habitat under at least partially closed canopy. However, the web orientation on trees appears to be indicative of closed versus partially open canopy forest.

Conservationists may benefit from utilizing the available arthropod data in assessing the quality of tropical forests. The ecology of obligate arboricolous orb-weaving spiders (like the nephilids *Clitaetra* and *Herennia*), seems especially well suited for systematic conservation assessments in the (sub)tropics because they range from western Africa (Kuntner 2006) through South and Southeast Asia into Australasia (Kuntner 2005) where some species are narrow endemics and others appear to be widespread and invasive (Kuntner 2005, 2006). The "Africa + Asia + Australasia" tropical belt matches the maps of global biodiversity conservation priorities (Brooks et al. 2006), but also lies precisely in a zone of high population pressure and low human development index (see Jha & Bawa 2006), a detrimental combination of factors associated with heavy deforestation.

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Differential survival of *Geolycosa xera archboldi* and *G. hubbelli* (Araneae, Lycosidae) after fire in Florida scrub

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Abstract. A replicated pre- and post-burn study of survival of small and large *Geolycosa xera archboldi* McCrone 1963 and *G. hubbelli* Wallace 1942 in Florida scrub was conducted. These two syntopic species were chosen because *G. x. archboldi* prefers large gaps of barren sand in the scrub matrix, sites with little fuel for fires, whereas *G. hubbelli* strongly favors small gaps having some leaf litter, sites with modest or high fuel-loads. On the basis of these species-specific differences in microsite characteristics, I hypothesized that *G. x. archboldi* would be very fire tolerant but that *G. hubbelli* would be fire intolerant. I established two size classes for the *Geolycosa*: small spiders had 3–5 mm diameter \times 5–9 cm deep burrows; large spiders had > 6 mm diameter \times 10–17 cm deep burrows. Burrows of 25 spiders in each species \times size class were marked before a burn in seven burn units (= fire management areas) and survival or mortality of each occupant was ascertained over the course of 5 days post-burn. Thus, the experimental design was 2 species \times 2 size classes \times 7 burn units \times 25 replicates/burn unit ($n = 700$ spiders total). Survivorship was very high in small and large *G. x. archboldi* and in large *G. hubbelli* (93–96%), but it was low in small *G. hubbelli* (35%). Temperature recordings suggest mortality in small *G. hubbelli* was caused by high temperatures at depths of 5–10 cm during intense, but brief burns that characterize fires in Florida scrub. In contrast, large *G. hubbelli* had burrows sufficiently deep so that most of them did not experience lethal temperatures during burns.

Keywords: Burrowing wolf spiders, endemism, Lake Wales Ridge, body size, fire ecology

Florida scrub is a fire-prone ecosystem confined to ancient sand ridges in the peninsular part of the state. This ecosystem also supports biotic communities that comprise a globally important, imperiled center of endemism (Deyrup 1989; Deyrup & Eisner 1993; Dobson et al. 1997; Menges 1999; Marshall et al. 2000; Estill & Cruzan 2001; Weekley et al. 2008). Presumably, as part of the suite of characters needed to survive in scrub, endemic species have evolved adaptations to frequent landscape-level burns that rapidly consume the leaf litter and standing vegetation. For example, the dominant woody shrubs have most of their biomass below ground, so they survive and quickly regenerate the shrub matrix by sprouting. In contrast, most endemic herbs are killed by fire and post-burn increases in abundance are due to seedling recruitment (Weekley & Menges 2003, and references therein). Scrub animals have three common methods for coping with fire at a landscape scale. On the one hand, some such as sand skinks (*Plestiodon reynoldsi*), gopher tortoises (*Gopherus polyphemus*), and flightless pygmy mole crickets (*Neotridactylus archboldi*), persist in place by exploiting a subterranean life style in the sandy soils (Robbins & Myers 1992; Deyrup 2005). On the other hand, the Florida scrub jay (*Aphelocoma coerulescens*) and other highly dispersive animals flee the oncoming flames on wing or foot and settle in unburned scrub (Robbins & Myers 1992). A third approach, one used by weak-flying insects and arboreal spiders, such as the red widow spider (*Latrodectus bishopi* Kaston 1938), is to experience high mortality during a burn and to recolonize subsequently from nearby, unburned refugia (Deyrup & Eisner 1996; Carrel 2001, 2008).

Two species of rare burrowing wolf spiders, *Geolycosa xera archboldi* McCrone 1963 and *G. hubbelli* Wallace 1942, are

endemic to oak scrub on the Lake Wales Ridge in the middle of peninsular Florida (Marshall et al. 2000). Because the spiders spend most of their lives below ground in tubular burrows they construct in the sand, I expected that they might be fire tolerant, similar to other subterranean animals. But knowing that small individuals build much shallower burrows than larger, older individuals (Table 1 and Figure 1), I hypothesized that survival of a burn in *Geolycosa* might be size dependent because smaller spiders build more shallow burrows than larger spiders and, as a result, small spiders could be more exposed to lethal temperatures that penetrate the upper layer of soil when scrub is burned. In addition, because *G. x. archboldi* prefers large ($> 1 \text{ m}^2$), barren gaps of sand and does not decorate its burrow entrance with a turret, whereas *G. hubbelli* favors small gaps ($\sim 0.1 \text{ m}^2$) in the shrubby matrix having leaf litter from which it obligatorily builds a turret (Carrel 2003a, b), I also hypothesized that the latter species might be more likely to perish in a fire. To test these ideas, I conducted a pre- and post-fire study of survival (or mortality) of individual *G. x. archboldi* and *G. hubbelli* in two size classes (small and large individuals, Tables 1 and 2) over the course of several burn events in Florida scrub. I also collected ambient temperature data in *Geolycosa* burrows and on the soil surface during a fire. To my knowledge this is the first replicated, quantitative study of survivorship in any spider exposed to burning of its habitat, and it may be one of the few such studies with any terrestrial arthropod to date (Warren et al. 1987; Whelan 1995; Siemann et al. 1997; Swengel 2001).

METHODS

Study site.—I conducted a pre- and post-fire study of *Geolycosa* survival in flat, oak scrub at the 2101 ha Archbold Biological Station, in southern Highlands County, Florida (elev. 36–46 m, 27°11'N, 81°21'W). The work was performed in the most extensive vegetative association, called scrubby

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Table 1.—Depth and volume of burrows constructed by small and large *Geolycosa* spiders. Typical data were calculated using best-fit regression equations published by Carrel (2003a).

Spider species	Burrow properties	Burrow size class (diameter, mm)	
		Small (3–5)	Large (6–15)
<i>G. xera archboldi</i>	Depth (cm)	4.6–8.2	10.0–15.4
	Volume (cc)	0.4–2.3	4.5–19.7
<i>G. hubbelli</i>	Depth (cm)	5.6–9.1	10.3–16.6
	Volume (cc)	0.7–2.8	4.5–49.0

flatwoods, which has fire-resistant slash pines (*Pinus elliotii*) scattered in a dense matrix dominated by low-growing shrubby oaks (*Quercus inopina*, *Q. chapmanii*, and *Q. geminata*), palmettos (*Serenoa repens* and *Sabal etonia*, Arecaceae), and shrubby lyonias (*Lyonia ferruginea*, *L. fruticosa*, and *L. incida*, Ericaceae) (Abrahamson et al. 1984). For management purposes, the scrub at Archbold is organized into a series of 187 burn units and a detailed history of burning in each unit is available (Main & Menges 1997; unpublished Archbold records). I was able to work in seven units, ranging in size from 4.6 to 66.5 ha, two of which were burned in February 2001, one in October 2002, two in July 2007, and two in August 2007. Voucher specimens of both *Geolycosa* species were deposited in the Invertebrate Collection at Archbold.

Experimental design.—I haphazardly located 25 small (3–5 mm diam.) and 25 large (6–15 mm diam.) burrows of both

Table 2.—Attributes of two *Geolycosa* species placed into two size classes (small and large) based on diameter of their burrow openings, for study of survivorship after fire. Typical data were calculated using best-fit regression equations (Carrel 2003a). Sample size in this study (*n*) for each species \times size class is also given.

Spider size class		<i>G. x. archboldi</i> (turret absent)	<i>G. hubbelli</i> (turret present)
Small	Burrow diameter (mm)	3–5	3–5
	Carapace width (mm)	1.4–2.3	1.5–2.1
	Body mass (mg)	8–30	8–17
	Sample size (<i>n</i>)	175	175
Large	Burrow diameter (mm)	6–10	6–15
	Carapace width (mm)	2.7–4.3	2.4–5.1
	Body mass (mg)	40–230	25–600
	Sample size (<i>n</i>)	175	175

Geolycosa species by visually searching in seven different burn units 1–2 days before each was burned. Burrows were > 10 m from the perimeter of a burn unit to avoid edge effects, particularly kerosene-induced flames from drip torches used to ignite the leaf litter and vegetation. In previous studies (Carrel 2003a) I showed that the persistently open, circular burrows render these spiders very detectable: by conducting a rapid, but thorough visual search of an area (10–100 m²), one typically locates 90–95% of individuals actually present. Furthermore, the presence or absence of a turret constructed from leaves and debris, held in place with silk around the burrow opening, is a reliable tool for telling the species apart (Carrel 2003a). In addition, burrow diameter, as measured with calipers to the nearest 0.1 mm, is a highly reliable surrogate for the size of the occupying spider as well as the depth and volume of its burrow (Tables 1 and 2).

Before a burn, I marked the location of each spider burrow (*n* = 700 total) by placing two thin metal stakes vertically in the sand ~10 cm on opposite sides of the burrow entrance. Following a burn, I revisited each burrow for 5 consecutive days and determined if the resident spider was alive. I used four criteria for survivorship: sighting of a spider sitting near the top of its burrow; luring a spider from the burrow by the presence of insect prey that I tethered on a thread near the entrance; restoration of a damaged burrow entrance or turret; and placement of newly excavated sand on the ground near a burrow. If all these criteria were negative, on the fifth or sixth day post-fire I carefully excavated a spider's burrow looking for its body. In so doing I could confirm that the burrow was occupied by a spider and, based on the soft, decomposing condition of a corpse, that the resident individual perished during or shortly after the blaze.

Air and soil temperature measurements.—I used Hobo U-12 digital dataloggers (Onset Computer Corporation, Pocasset, Massachusetts) fitted with Type K thermocouples to record air and soil temperatures in the scrub, following the established protocols of Wally et al. (2006). After calibrating each machine, I programmed the dataloggers in the laboratory to record one reading per second and to output maximum temperatures at 1 min intervals prior to deployment in the scrub. I obtained two sets of temperature data: maximum daily temperatures inside *G. x. archboldi* burrows and nearby

Geolycosa xera archboldi

Geolycosa hubbelli

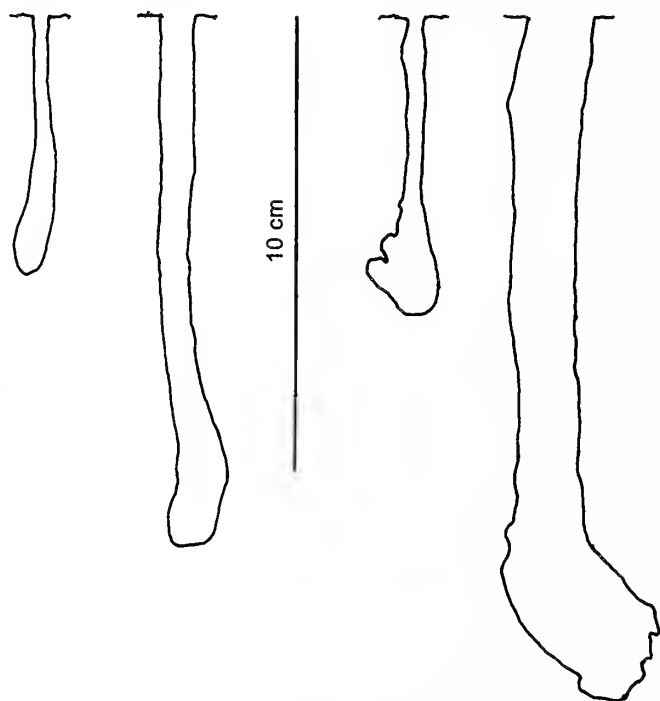


Figure 1.—Silhouettes of small and large burrows of *Geolycosa xera archboldi* and *G. hubbelli* prepared from representative plaster casts (Carrel 2003a). Note interspecific difference in the architecture of burrow bases.

in undisturbed soil on hot, sunny days; and the intensity and duration of fire at point sites on the soil surface in oak scrub in order to gain a better perspective of the thermal dynamics experienced by subterranean spiders.

The first set of temperature recordings was designed to determine whether the open burrows of small and large *G. x. archboldi* under typical summer daytime conditions were significantly warmer than intact soil at comparable depths in the scrub. I chose to study only *G. x. archboldi* because this species occurs predominantly in large, barren gaps of unshaded sand where solar heating is the most intense in scrub. In contrast, *G. hubbelli* is typically found in small gaps with leaf litter on the sand, so its burrows are insulated from solar heating both by the leaf litter and by shade cast by the surrounding shrub matrix. Thus, my reasoning was that if maximum daytime temperatures in open *G. x. archboldi* burrows were comparable to those in undisturbed soil at comparable depths, then a similar burrow/soil equivalency probably would hold for *G. hubbelli* (even though the maxima obviously would be smaller). (Subsequent measurements showed this relationship was valid, JEC unpubl. data.) Over the course of 3 weeks in late August–early September 2007 I simultaneously set up ten replicate sets for 1 day each with thermocouples in five different positions: at 0, 5 cm, and 10 cm depth in intact sand and at the bottom of small (3–5 mm diam. \times 3.5–5.2 cm depth) and large (6–12 mm diam. \times 10.5–14.3 cm depth) *G. x. archboldi* burrows after the resident spiders were removed. Maximum daily air temperatures at 1.5 m above ground were also obtained at the official Archbold weather station on the days that soil temperatures were recorded.

Secondly, in an attempt to characterize the intensity and duration of a fire in oak scrub, I acquired data on soil surface temperatures during a “category 3” burn in August 2007 from the plant ecology group at Archbold. (“Category 3”, the highest intensity in the classification scheme used by Archbold staff, means that most surface litter was consumed, all leaves of palmettos and shrubs 0–2 m elevation were completely consumed, and small twigs on shrubs were consumed in a blaze.) Following their published protocol (Wally et al. 2006), many thermocouples attached to dataloggers were placed in contact with the soil surface at a variety of locations to record soil surface temperatures during a burn event. Using data from ten dataloggers in sites that experienced heavy burns, I normalized the temporal records so that the peak maximum temperatures all occurred at the 10 min mark, so that there would be several min of pre-burn data as well as ≥ 30 min post-maximum peak data. By definition, ignition threshold is $> 60^\circ\text{C}$ and cessation of fire is set at $\leq 60^\circ\text{C}$; the 60°C benchmark is used because it corresponds to the temperature at which plant cell death occurs (Wally et al. 2006, and references therein).

Statistical analyses.—I used the General Linear Models program of SPSS to perform ANOVA to evaluate the significance of variables in the sets of data on spider survival (SPSS 2005). The Levene test statistic was calculated to confirm that the variance did not differ significantly between the groups ($P > 0.05$). Differences in post-burn survivorship of spiders were analyzed by Chi square tests with Yates correction for small sample size (X^2_c , Simpson et al. 1960).

Table 3.—Effect of burn event, species identity and body size of spiders (as measured by burrow diameter) on post-burn survival of two *Geolycosa* species in Florida scrub.

Source of variation	df	MS	F	P
Burn event	6	0.178	1.966	0.068
Species	1	14.573	160.9	< 0.001
Size of spider	1	18.241	201.4	< 0.001
Species \times size	1	15.156	167.3	< 0.001
Error	672	0.091		

I calculated the average (mean \pm SE, $n = 10$) and range of maximum daily temperatures at all five locations in soil and in the air. I used the General Linear Models program of SPSS to perform univariate ANOVA to evaluate the significance of location in data on soil temperatures. The Levene test statistic was calculated to confirm that the variance did not differ significantly between the groups ($P > 0.05$). Subsequently I performed two post hoc multiple range tests (Student-Newman-Keuls (SNK) and Tukey HSD) to determine in a pairwise fashion which locations had significantly different temperatures (P set at 0.05) (SPSS 2005).

After normalizing the soil surface temperature data during one burn event so that temperatures peaked at all locations ($n = 10$) in the 10th minute, I calculated the minimum, mean, and maximum temperature minute by minute for 30 min.

RESULTS

Post-burn survival of *Geolycosa* species.—Spider species, spider size, and spider species \times spider size interaction were all highly significant variables determining the post-burn survival of *Geolycosa* species (Table 3). This meant that there was a complex interaction between spider species identity and spider size that required further analysis. Fortunately, as there were no significant differences among the seven burns according to the AVOVA results (Table 3), I was able to combine the data and delete “burn event” as a variable, which greatly simplified further analyses. As shown in Table 4, few small *G. hubbelli* (35.4%) survived the burns. In contrast, I found almost all large *G. hubbelli* (94.5%) and almost all *G. xera archboldi* regardless of size (small = 93.1%, large = 96.0%) were alive 5 days post-burn in the scrub. The intraspecific, size-dependent difference in survivorship for *G. hubbelli* was highly significant ($X^2_c = 133.49$, $df = 1$, $P < 0.0001$).

Maximum daily temperatures in *G. x. archboldi* burrows.—On ten sunny days in late summer 2007, maximum air temperatures at the Archbold weather station were hot, averaging $34.6 \pm 0.3^\circ\text{C}$ (mean \pm SE, range 33.3 – 36.1°C),

Table 4.—Survivorship of *Geolycosa* spiders as a function of burrow/body size and species identification. Results of statistical analyses (Chi square test with Yates correction for small sample size, X^2_c) for intraspecific size-based differences in survival are given.

Species	% Surviving		X^2_c	P
	Small ($n = 175$)	Large ($n = 175$)		
<i>G. xera archboldi</i>	93.1	96.0	0.89	NS
<i>G. hubbelli</i>	35.4	94.5	133.49	< 0.0001

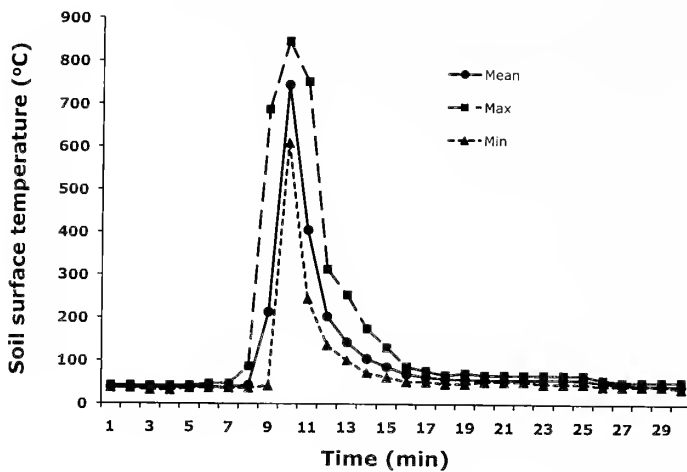


Figure 2.—Intensity and duration of a fire at a point source in Florida scrub. Note rapid onset and rise to peak temperature at soil surface, followed by somewhat less rapid decline. See methods for details.

but the maximum daily temperature on the surface of fully exposed sand in scrub was much greater: nearly 16°C hotter (51.2 ± 0.9 , $47.8\text{--}56.4^{\circ}\text{C}$). Univariate ANOVA showed there was a significant difference among the soil temperature data by location ($F_{4,45} = 3.599$, $P = 0.013$). Post hoc analysis revealed that, despite intense solar heating, the maximum daily temperatures at the bottoms of spider burrows and down in undisturbed soil remained significantly lower than at the surface (SNK and Tukey HSD tests, $P < 0.05$). Small, shallow spider burrows got as warm as soil at 5 cm depth (burrow: 38.5 ± 0.4 , $36.7\text{--}40.3^{\circ}\text{C}$; soil: 37.8 ± 0.5 , $35.7\text{--}40.0^{\circ}\text{C}$; $P = 0.44$). In addition, large, deep spider burrows stayed even cooler ($P < 0.05$) than shallow ones during the day and their maximum daily temperatures were the equivalent to those in soil at 10 cm depth (burrow: 33.3 ± 0.4 , $31.0\text{--}36.0^{\circ}\text{C}$; soil: 34.1 ± 0.4 , $32.7\text{--}36.0^{\circ}\text{C}$; $P = 0.28$). Hence, despite the fact that the spiders' burrows remained constantly open, the most extreme thermal climate experienced by resident animals if they were deep in the burrows would be virtually the same as if they were buried in undisturbed soil at a comparable depth, far less than that at the burrow entrance.

Soil surface temperature during a burn.—The time course of a burn in the scrub at any point in the burn unit was remarkably rapid. As shown in Fig. 2, the fire went from ignition temperature (60°C by definition) to peak maximum soil temperature ($609\text{--}846^{\circ}\text{C}$) in ≤ 2 min, then it declined to $\sim 60^{\circ}\text{C}$ in another 7 min. Hence, from the perspective of a *Geolycosa* hiding in its burrow, the fire lasted ≤ 10 min.

DISCUSSION

Mortality in *G. hubbelli*.—The results were generally in agreement with my initial hypotheses with one exception: the post-burn survivorship of large *G. hubbelli* was much greater than expected. In fact, to my surprise, it matched that for small or large *G. x. archboldi* (93–96%). I suspect burrow architecture makes large *G. hubbelli* very fire tolerant. As *G. hubbelli* grow they construct burrows that are not only wider in diameter and deeper, but also they excavate increasingly large, ovoid chambers at the bottoms (Table 1 and Fig. 1).

Such bulbous refugia ≥ 10 cm below the surface evidently protect large *G. hubbelli* from the brief but intense fires in the leaf litter and shrubbery above them, probably because the intense heat fails to penetrate to this depth.

I think the cause of mortality in small *G. hubbelli* is not fire-induced asphyxiation. Under natural conditions in sandy Florida soils, extensive measurements of prevailing gases in ~ 16 cm deep burrows occupied by a closely related burrowing wolf spider, *G. micranopy* Wallace 1942, showed no significant increases in CO_2 or decreases in O_2 concentrations relative to ambient atmospheric values (Anderson & Ultsch 1997). Thus, during a fire in Florida scrub, I doubt there would be extensive depletion of oxygen down in the spiders' porous burrows. Moreover, detailed physiological studies by Prestwich (1983a, b; 1988a, b) have demonstrated that active Florida spiders rely mostly on anaerobic metabolism because nearly all of their tissue phosphagen is quickly (within 10–15 s) depleted after onset of activity. Hence, a 10-min period of hypoxia during a fire in Florida scrub should, at best, present *Geolycosa* spiders at rest in their burrows only with a mild respiratory challenge.

I suspect the primary cause of fire-induced mortality in small *G. hubbelli* is high temperature in surficial soils and burrows. Field measurements show that soil temperatures at 2–3 cm depth rise to 80°C during intense fires in scrub, and at depths ~ 5 cm the temperature may reach 65°C when fuel-loads are modest (< 0.6 kg dry leaves and stems on the ground/ m^2) (Hierro & Menges 2002; Alexis et al. 2007). However, if the fuel-load on the ground in Florida scrub is high (~ 1 kg/ m^2), as often is the case near burrows of *G. hubbelli*, then maximum soil temperatures at 5 cm depth during a burn are very hot ($88 \pm 9^{\circ}\text{C}$) (Hierro & Menges 2002). Several other studies have reported similar relationships between fuel load and soil temperature profiles (Whelan 1995). Hence, the relatively shallow burrows of small *G. hubbelli* probably reach temperatures that exceed the upper lethal temperatures of spiders, which range from 45 to 55°C for most species (Pulz 1987; Hanna & Cobb 2007).

Assessment of fire effects on *Geolycosa* populations.—The strengths of this study are: 1. burn events were true replicates spanning 7 months of the calendar year; 2. pre- and post-burn sampling of many ($n = 700$) individual spiders was conducted; 3. sampling was size-based and quantitative. These attributes set it apart from almost all other previous studies that suffer from no replication or pseudoreplication and from nonquantitative or semiquantitative sampling methods (Warren et al. 1987; Siemann et al. 1997; Swengel 2001; van Mantgem et al. 2001; Hanula & Wade 2003). However, as explicitly pointed out by Whelan (1995), this study did not involve censuses of burrowing wolf spider populations before and after fires at randomly chosen sites. Thus, I cannot make any conclusions about whether fire has a significant impact on *Geolycosa* populations in Florida scrub. But the data in this study suggest fire probably is not at all deleterious to populations of *G. x. archboldi* and it may have only a weak negative effect in the short-term on *G. hubbelli* populations. Long-term studies still in progress will address this subject (JEC, unpubl. data).

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BOOK REVIEW

Harvestmen: the Biology of Opiliones. Edited by Ricardo Pinto-da-Rocha, Glauco Machado and Gonzalo Giribet. 2007. Harvard University Press, Cambridge, Massachusetts. 597 pp. ISBN 13:978-0-674-02343-7. US\$125.

Except for some of the very small orders, nearly all arachnids have now received at least a first book on "The Biology of..." It is a curious question why it took so long for such a book to appear on the third most diverse order, Opiliones. But here it is at last, and it proves to be well worth the wait. Twenty-five authors have contributed to 15 chapters which summarize virtually everything that is known about harvestmen up to 2006. The organization of the book follows the general pattern: there are chapters on morphology, phylogeny and biogeography, systematics and paleontology, ecology, feeding, enemies and defense, reproduction, development, and social behavior. Each of the chapters is meticulously researched and, rather than simply recounting what is in the literature, the authors have synthesized and analyzed what they found. The result is that each chapter is an original review article that in itself is a significant contribution. Henceforward it will not be possible to write about or research harvestmen without referring to this book. And interestingly, the preponderance of South Americans among the chapter authors signals an important shift: the center of research on this group of arthropods has moved south, perhaps propelled by the enormous diversity in the group to be found in tropical America.

A number of the chapters were of particular interest to this reviewer, especially the one on systematics by Pinto-da-Rocha and Giribet (it is also worth noting that one or the other of the editors has co-authored nine of the fifteen chapters in the book). This chapter is extraordinarily complete. Not only are keys to taxa included, but each described family is discussed in detail and abundantly illustrated. Keys are useful especially in the suborder Laniatores, where much reshuffling of families has taken place in the last decade. Reference is frequently made in these discussions to advances in our understanding of harvestmen systematics using phylogenetic data based on new molecular evidence. Areas requiring attention, such as the possibly paraphyletic family Ceratolasmatidae, are clearly pointed out. An overview of the current state of classification is given in a four-page table, covering the subfamily level, which also gives the numbers of genera and species currently included in each. Readers with long memories will recall that Ernst Mayr, in a text on taxonomy, used Opiliones as an example of an "over-split" group with, on average, less than two species per genus. The problem still exists in some places;

the subfamily Tricommatinae has 51 species in 29 genera! Only one small quibble with this chapter—some of the many scanning electron micrographs used for illustrations are printed too small.

The chapter on defense mechanisms is another gem, especially the section on chemical defenses, a signature feature of harvestmen biology. Here again, a useful chart puts in one place all the molecules and the species that produce them (except for the 22 gonyleptids studied by Hara et al. [2005]), and a quick perusal of that chart points the way for future work. Why, for example, does the single phalangiid studied so far (*Phalangium opilio* L. 1761) produce naphthoquinones, while the supposedly closely related sclerosomatine *Leiobumma* species produce long-chain alcohols and ketones? Research in the ecological chemistry of harvestmen has so far been focused on gonyleptomorph Laniatores, all of which produce a mixture of benzoquinones (at least 37 different molecules), while the chemistry of the defensive secretion is not known for even a single member of the Dyspnoi and is known for only one travunioid, *Sclerobumma nondimorphicus* Briggs 1971. Clearly this is an area of research where discoveries are waiting to be made, and one which I am currently exploring with a chemist colleague.

Finally, it was fun to read the table on pp. 2–3, which lists vernacular names for harvestmen from more than 30 countries. Predominant are names that refer to harvest time, the long legs of the most obvious members of the order, and their perceived similarity to spiders. We also learn that it is only in Finnish in which the name for a species of Opiliones, *lukki*, means exactly that.

This is an important and excellent book which should be in every arachnologist's library, and which will be indispensable for university and departmental libraries.

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SHORT COMMUNICATION

A new species of *Xysticus* (Araneae, Thomisidae) from Alberta, Canada

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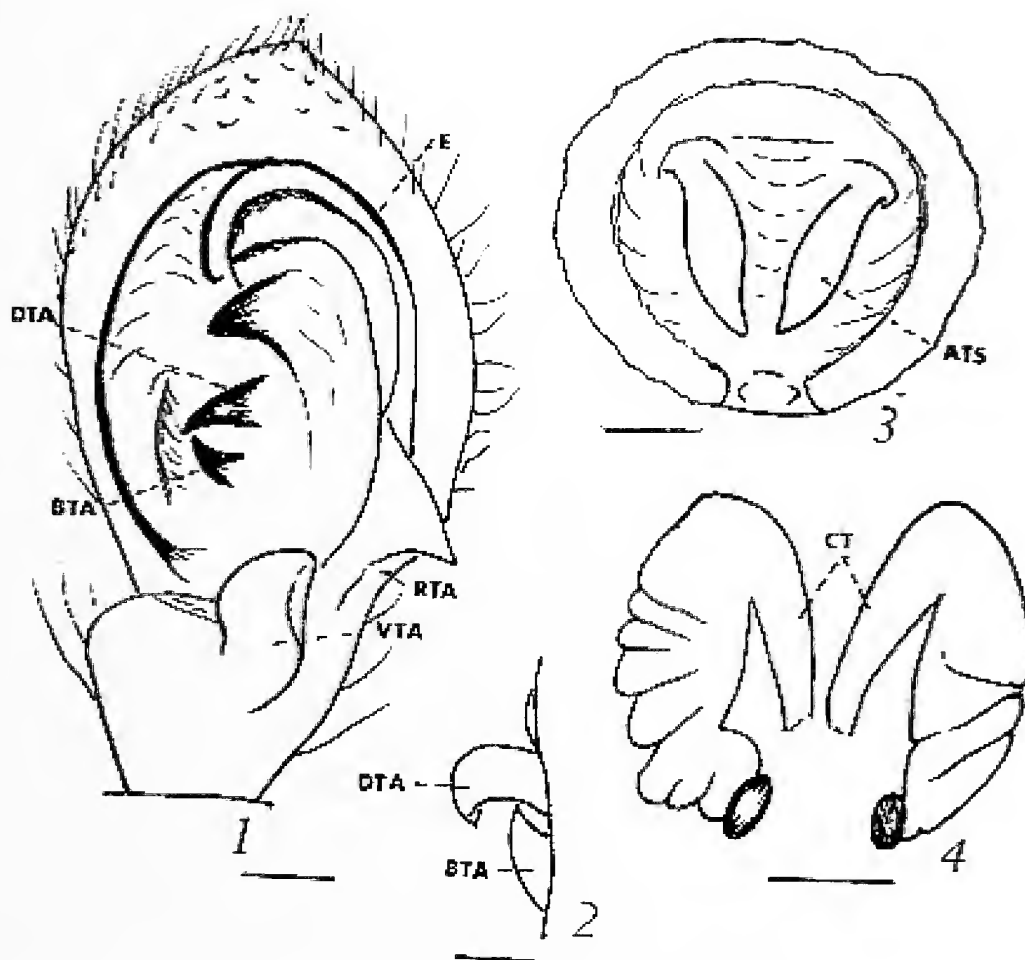
Abstract. A new species of the crab-spider genus *Xysticus* (Thomisidae), *X. albertensis*, is described from northern Alberta, Canada. Specimens are compared with those of three species that closely resemble them and live in the same geographical region, namely, *X. chippewa* Gertsch 1953, *X. canadensis* Gertsch 1934, and *X. britcheri* Gertsch 1934.

Keywords: Taxonomy, crab spider, western Canada

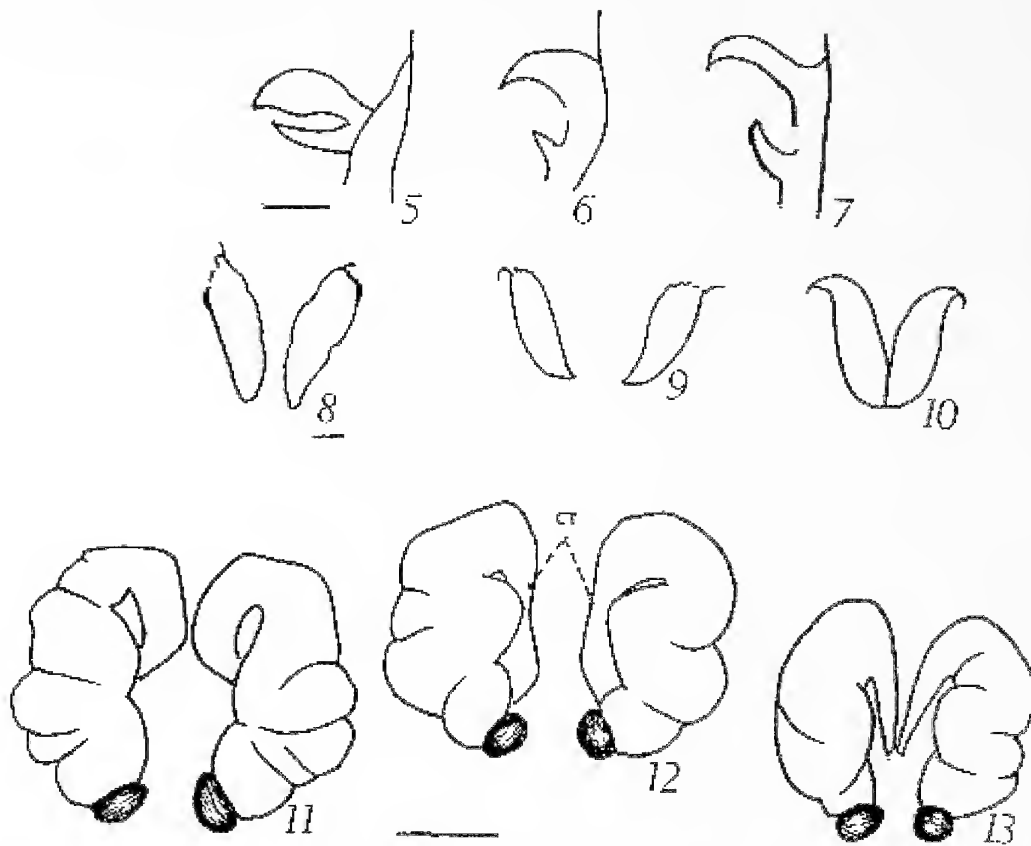
The crab-spider genus *Xysticus* C.L. Koch 1835 was established for the widespread Palearctic species *X. andax* (Schrank 1803), and is currently regarded as a major world entity comprising more than 300 species (Platnick 2007). North America is home to nearly 70 species, a possible six of which are regarded as Holarctic (Dondale 2005; Dondale et al. 2006). The purpose of the present contribution is to describe a new species from northern Alberta, Canada, individuals of

which closely resemble those of three species that are found in the same region, namely, *X. chippewa* Gertsch 1953, *X. canadensis* Gertsch 1934, and *X. britcheri* Gertsch 1934.

Specimens are lodged in the following institutions: Canadian National Collection of Insects & Arachnids, Ottawa, Ontario, Canada (CNC); Strickland Entomological Museum, University of Alberta, Edmonton, Alberta, Canada (SEM).



Figures 1–4.—*Xysticus albertensis* new species: 1. Palpus of holotype, ventral view; 2. Tegular apophyses of same, retrolateral view; 3. Epigynum of paratype, ventral view; 4. Spermathecae and copulatory tubes of same, dorsal view. ATS, atrial sclerite; BTA, basal tegular apophysis; CT, copulatory tube; DTA, distal tegular apophysis; E, embolus; RTA, retrolateral tibial apophysis; VTA, ventral tibial apophysis. Scale bar for Figures 1, 3, 4 = 0.20 mm, for Figure 2 = 0.08 mm.



Figures 5–13.—5–7. Tegular apophyses of male palpi, retrolateral view: 5. *Xysticus chippewa* Gertsch; 6. *X. canadensis* Gertsch; 7. *X. britcheri* Gertsch. 8–10. Atrial sclerites of female epigyna, ventral view: 8. *X. chippewa*; 9. *X. canadensis*; 10. *X. britcheri*. 11–13. Spermathecae and copulatory tubes, dorsal view: 11. *X. chippewa*; 12. *X. canadensis*; 13. *X. britcheri*. CT, copulatory tubes. Scale bar for Figures 5–7 = 0.08 mm, for Figures 8–10 = 0.04 mm, for Figures 11–13 = 0.20 mm.

Family Thomisidae Sundevall 1833

Genus *Xysticus* C.L. Koeh 1835

Type species.—*Aranea audax* Schrank, 1803, original designation

Xysticus albertensis new species

Figs. 1–4

"*Xysticus* sp. 1": Nordstrom & Buckle 2004:9.

Type specimens.—Holotype male, paratype male, and paratype female from the margin of a small lake unofficially named "Esker Lake" by the collector, situated between Colin Lake (59°34'N, 110°08'W) and Woodman Lake, in Colin-Cornwall Wildland Park, Alberta, Canada, 6–9 July 2002, Ted Johnson (CNC). Paratypes: 1 male, 1 female, with same data (CNC); 2 males, with same data (SEM).

Etymology.—The name of the new species is derived from that of the Canadian province in which the type-series was collected.

Diagnosis.—Individuals of *X. albertensis* new species closely resemble those of *X. chippewa*, but also bear some resemblance to those of *X. canadensis* and *X. britcheri*, the last three of which are currently treated as Holarctic. All four are characterized by the possession of a smoothly curved distal tegular apophysis that is neither angulate nor "heeled" (Figs. 1, 2, 5–7). Males of *X. albertensis* are distinguished from those of the other three species by the basally stout and abruptly hooked distal tegular apophysis (compare Fig. 2 with Figs. 5–7). Also, the two tegular apophyses in male *X. albertensis* are narrowly separated, whereas these structures in the other three species are more separate. Females of the four aforementioned species are characterized by possession of posteriorly converging atrial sclerites (Figs. 3, 8–10). Individuals of *X.*

albertensis differ from those of *X. chippewa* and *X. canadensis* by the possession of slender copulatory tubes (compare Fig. 4 with Figs. 11, 12) and from those of *X. britcheri* by thicker copulatory tubes (compare Fig. 4 with Fig. 13). The atrial sclerites of *X. albertensis* are only moderately separated posteriorly (Fig. 3), whereas those of female *X. canadensis* are well separated (Fig. 9), and those of *X. britcheri* are touching (Fig. 10). Individuals of both sexes of *X. albertensis* are predominantly dark brown (much as in *X. britcheri*), whereas those of *X. chippewa* and of *X. canadensis* are much paler.

Description.—*Holotype male*: (Figs. 1, 2). Total length 3.98 mm; carapace 2.49 mm long, 2.16 mm wide. Carapace brown on yellowish background. Legs similar to carapace in color, paler distally; femur I with 8 erect macrosetae on prolateral surface. Sternum with many small round reddish brown conjoined spots. Abdomen dorsally with extensive dark brown areas; venter pale, with scattered reddish spots. Palpal tibia with stout tapered retrolateral apophysis and thick angular ventral apophysis; embolus moderately thick basally, slender distally, with free part separated from tegulum by distinct broad space distal to tegular apophyses; distal tegular apophysis thick at base, abruptly curved at tip, tapered to sharp point; basal tegular apophysis short, curved.

Paratype female: (Figs. 3, 4). Total length 5.31 mm; carapace 2.41 mm long, 2.16 mm wide. Color much as in male, but somewhat paler, with eye area and median area of carapace creamy white; abdomen with only a few reddish or dark brown spots. Leg macrosetae as in male. Epigynum with shallow atrium; atrial sclerites converging posteriorly, moderately separated at posterior end (Fig. 3). Copulatory tubes approximately two-thirds as long as spermathecae; spermathecae shallowly lobed (Fig. 4).

Variation.—Males, $n = 3$: Total length 3.82–4.32 mm; carapace 2.49–2.57 mm long, 1.99–2.22 mm wide.

Distribution.—Known only from the type locality.

ACKNOWLEDGMENTS

Donald J. Buckle first recognized *Xysticus albertensis* as new to science and kindly passed the specimens to the author for description.

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SHORT COMMUNICATION

An easy method for handling the genus *Phoneutria* (Araneae, Ctenidae) for venom extraction

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Abstract. This paper describes an easy, cheap, and safe method of capturing and handling the medically important spider *Phoneutria* for venom extraction. The method does not injure or kill the spider and allows the extraction of pure venom.

Keywords: Armed spider, venomous spiders, vivarium

The venomous ctenid spiders of the genus *Phoneutria* (*P. uigriventer* Keyserling 1891) (Figure 1a) are medically important due to their aggressiveness (Fig. 1a), their great speed, and the dangerous effects of their venom (Bücherl 1953a). Consequently, researchers are interested in obtaining pure venom from these spiders so that the medical significance of its components can be explored. Traditionally, spiders have been immobilized using anesthesia (CO₂, chloroform, ether, or other substances) or with cold temperatures, but these techniques can cause mortality or alter the behavior and physiology of the animal (Harris et al. 1965; Randall 1982), with immediate or latent harmful effects (Nicolas & Sillans 1989). Furthermore, venom extraction following these handling methods has often entailed the excision and maceration of the entire venom gland, a procedure that produces impure venom (Bücherl 1953a). Bücherl (1953a) describes a technique that avoids these problems. It consists of irritating the spider so that it attacks and envenomates a device (two pipettes connected with an elastic surgical tube) from which the venom can be extracted. This may be the safest method for the extractor and does not cause the animal's death, but the process is laborious and does not produce a sufficient amount of venom.

Here we propose an easy, cheap method for capturing and handling *Phoneutria* for venom extraction that is safe for both the extractor and the spider. The handling device consists of a transparent or semi-transparent 2-liter plastic (PET) bottle (i.e., empty soft drink bottle) that has been cut transversely across the middle. Only the top half of the bottle is retained for use as a handling chamber (Fig. 1b). An 8-cm longitudinal slit is cut into the side of the handling chamber. Then, while holding onto the top of the bottle mouth (with lid), the chamber is placed over the spider, imprisoning it. At this point, the spider typically attempts to climb upward toward the neck of the bottle. Filter paper should be used as a floor to capture any venom released by the spider; the venom can be recovered later by washing the filter paper with an organic solvent (e.g., acetonitrile). The spider is forced away from the bottle wall or lid and onto the filter paper by gently tapping the chamber against the extraction bench. Once the spider is on the filter paper, a glass stirring rod is inserted through the

longitudinal slit and pushed down onto the spider in the area between the cephalothorax and the abdomen. This presses the spider onto the filter paper and immobilizes it (Figure 1c).

While continuing to press the animal down with the glass rod, the handling chamber is removed and the sides of the animal's cephalothorax are grasped between the index finger and thumb (Figure 1d). Once the spider is firmly grasped, the glass rod can be removed and the animal carried away for the venom extraction (Figure 1e). Venom extraction consists of placing electrodes against the region of the cephalothorax lying above the venom glands and then stimulating the spider with 6 V (Bücherl 1953b). The venom is collected from the chelicera in a small capillary tube (Smith & Micks 1968; Morris & Russell 1975) or on a glass plate.

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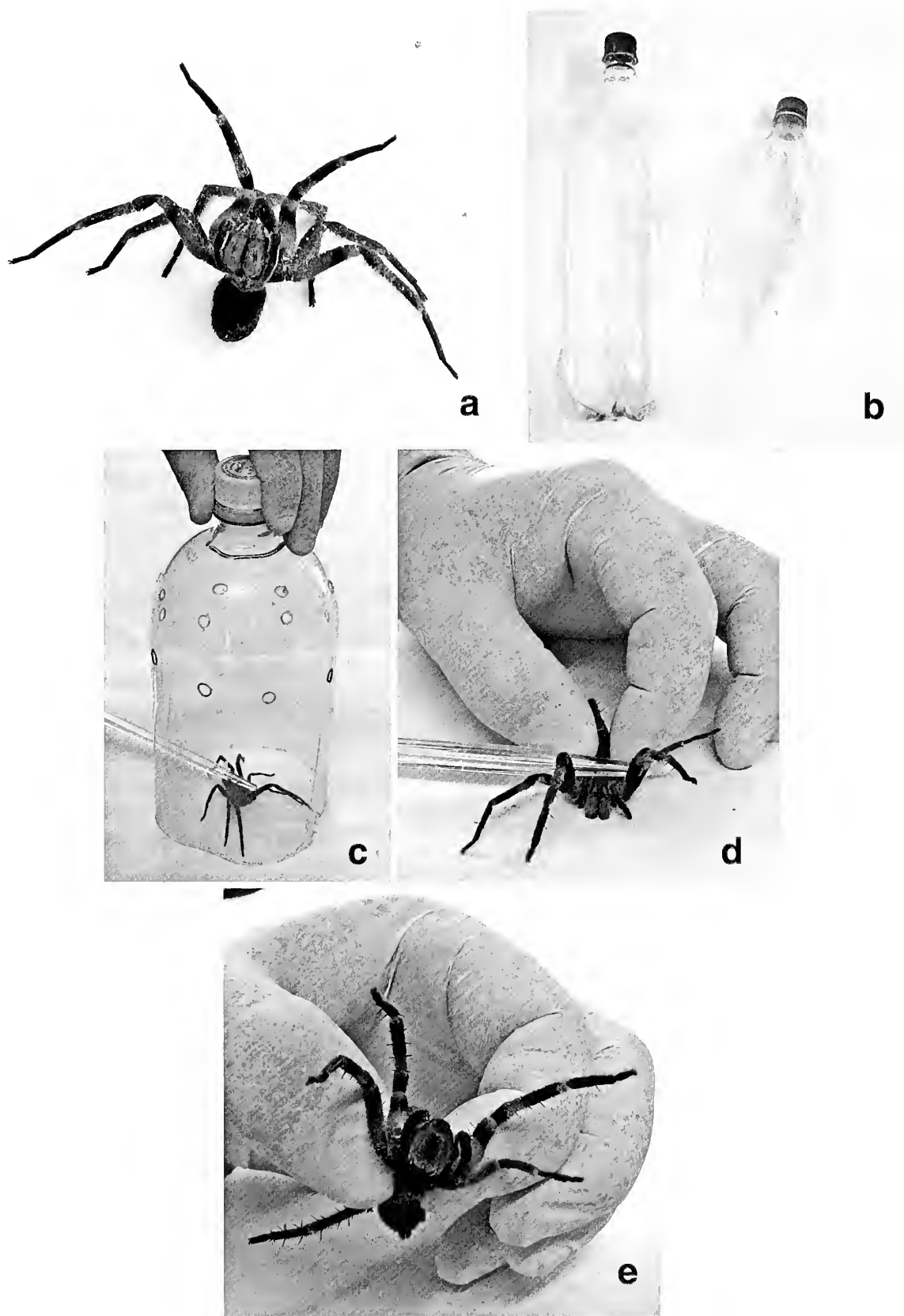


Figure 1.—The step-by-step handling method for venom extraction of *Phoneutria nigriventer*. a. The spider in an aggressive position; b. Left side of an empty 2-liter plastic bottle and right side of a bottle with a transverse cut and a glass stick inserted in the perpendicular cut; c. The trapped animal in the bottle being immobilized with the glass stick; d. Grasping the spider with fingers; e. Spider ready for venom extraction.

SHORT COMMUNICATION

Courtship behavior and copulation in *Tengella radiata* (Araneae, Tengellidae)

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Abstract. The first description of the courtship behavior and copulation is provided for *Tengella radiata* (Kulczynski 1909). The male courts the female by rocking his body and vibrating his abdomen. These behaviors seem to induce the female to move out from her retreat onto the sheet and incline her body to facilitate intromission. The female has an active role during the courtship: strumming the tunnel and sheet threads, apparently inducing the male to increase the frequency and intensity of his courtship. Palpal insertion is extremely short. The female terminates the copulation by lunging at the male.

Keywords: Courting, sexual selection, funnel web spider

Tengella radiata (Kulczynski 1909) has a wide distribution in Costa Rica where it inhabits mature and secondary wet forests and coffee plantations from 50 to 1500 m elev. (Wolff 1977; Santana et al. 1990, pers. obs.), but it is, nevertheless, unknown outside of this small country. Its web consists of a large, horizontal sheet with an upper tangle that contains some cribellate threads and a tunnel at the “interior” section of the sheet (Santana et al. 1990; Eberhard et al. 1993; Eberhard & Pereira 1993). Spiders rest near the tunnel opening during the day.

The sexual biology of this spider is completely unknown. In nature males occasionally co-inhabit webs with adult females (W.G. Eberhard pers. comm), and I have occasionally observed males near or on the sheet of possibly adult females. Here I describe for the first time the courtship behavior and copulation of *T. radiata* and compare these behaviors to those of some species within families of the *Tengella*’s sister groups lycosoids and agelenoids (Coddington 2005). The family is of interest because it is a cribellate member of the Lycosoidea.

Courtship behavior and copulation of two pairs of *T. radiata* were filmed using a digital video camera Sony DCR-VX 1000 (30 frames/s). Both females were virgins raised from eggs in captivity and maintained in plastic boxes (30 × 18 × 11 cm) where they constructed their webs. One female was paired with one male that was also raised in captivity from different parents. The second female was paired with an adult male collected in the field. Male pre-copulatory and copulatory courtship behavior and copulation are defined as in Eberhard & Huber (1998). Male courtship refers to those behaviors that induce the female to respond in a way that favors the male’s reproduction (Eberhard 1996). Copulation consists of all genitalic contact between a particular male-female pair, including the insertion of the embolus into the epigynal opening. It finishes when the pair separates from the copulatory position. Drawings were traced from video images. Spiders and egg sacs were collected near San Jose, Costa Rica; voucher specimens were deposited at the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica.

The first reaction of the male when placed on the female’s web was to walk on the sheet, more or less randomly at first and then toward the tunnel opening where the female rested. Following this movement, courtship and copulation can be roughly divided into three consecutive phases seen in both pairs: courtship by male, while the female is in the tunnel, with the result that the female moves out of the web tunnel; male courtship once the female is out on the sheet, presumably to induce the female to adopt the copulatory position; and copulation. The female responded to male courtship by either sending vibratory signals through the web threads, launching an

apparent attack toward him, or adopting the copulatory position (described below). In total, the courtship behavior and copulations of *T. radiata* lasted 57 min in one pair (5 copulations) and nearly 90 min (9 copulations) in the second pair. In both cases the female eventually expelled the male from the web.

When the male walked directly toward the tunnel opening, he stopped suddenly as the female began to strum the threads of the sheet with more or less alternate movements of her palps (Fig. 1). Strumming occurred in bouts of up to 20. During a strumming movement the female first extended both palps anteriorly and then flexed first one and then the other posteriorly, snagging some threads of the sheet with the tip of the palps. These sheet threads were pulled upward (visible in some video records) until they snapped free, possibly due to the tension. The palpal movements gave the impression of scratching the sheet surface rather than twanging particular threads.

The female strumming movements apparently induced the male to stop, at least momentarily. The male then responded by rocking his body vigorously in antero-posterior direction (Fig. 2). He stood with all his legs on the sheet and shook the sheet visibly as he moved (occasionally legs I were lifted while rocking). The rocking movement was produced primarily by the antero-posterior movement of the male’s body rather than by bending his legs and occurred in bouts of 3–5 rocking movements ($n = 12$). The male also frequently vibrated his abdomen once or twice just before a bout of rocking movements (5 out of 8 bouts in which illumination and angle were favorable). The female frequently stopped strumming the sheet (5 out of 7 sequences where both male and female were in focus); nearly immediately the male began to rock. If the female remained motionless after a rocking bout, the male often advanced a few millimeters toward her (2 of 8 instances). However, in most cases the female began again to strum the sheet as the male approached her, inducing him to stop and resume courtship. It seemed that in these cases the male rocked his body more vigorously before moving again toward the female that remained inside but near the tunnel opening. In one instance the female moved slowly out of the tunnel and stopped and strummed the sheet before continuing toward the male. The male rocked his body and advanced toward the female but she moved back a few millimeters and then darted at him in an attacking position (first legs slightly raised and directed forward and chelicerae spread). The male moved rapidly backward nearly 4 cm then began to rock his body again while the female returned to the tunnel.

In both pairs, after several separate bouts of rocking by the male (12 in one pair and 17 in the other), the female moved out of the tunnel, ceased strumming the sheet, and allowed the male to approach

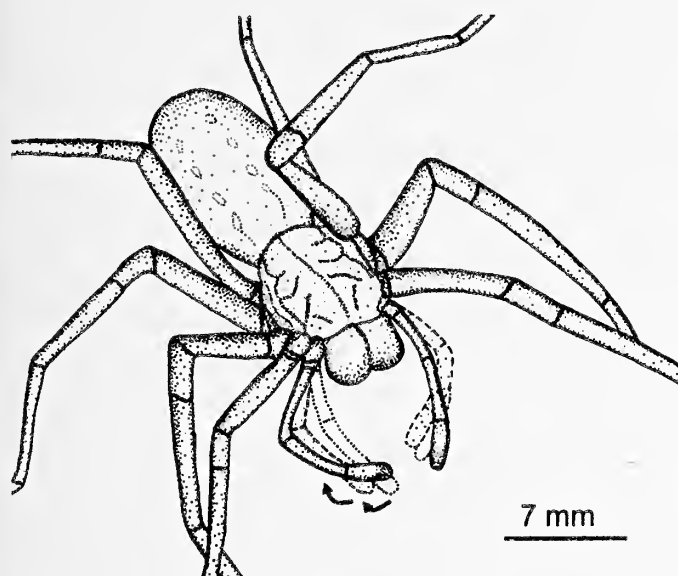


Figure 1.—Strumming movements of the female's palps on the sheet during courtship. Arrows show the sequence of the palps' movements: dots- initial position, dashed- subsequent position, solid-final position.

her. The male moved over the female's body so that they faced opposite directions, and as he did so she inclined her body laterally (Fig. 3), with her epigynum exposed (copulatory position). From this position the male repeatedly contacted the female's epigynum with one palp (Figs. 3, 4), while his other palp was held in front of his body. The male's extended palp moved rapidly to touch the epigynum briefly and then withdrew (mean duration of extend-contact-withdraw cycle = 0.11 ± 0.02 s, $n = 37$). These movements apparently correspond to "flubs" observed in other species (Watson 1991; Stratton et al. 1996; Huber 1998; Eberhard & Huber 1998). On two occasions where the complete sequences were observed, the male made 17 and 29 flubs before the palp engaged with the epigynum and the haematodocha was finally inflated. The insertions with haematodocha expansion lasted 0.38 s (± 0.16 , $n = 5$). The haematodocha remained inflated during the entire insertion ($n = 2$). On three occasions (2 in one pair and 1 in the other, where the angle and focus were appropriate), the male was observed to move his abdomen up and down in possible copulatory courtship movements. These movements were slower than the pre-copulatory courtship vibratory

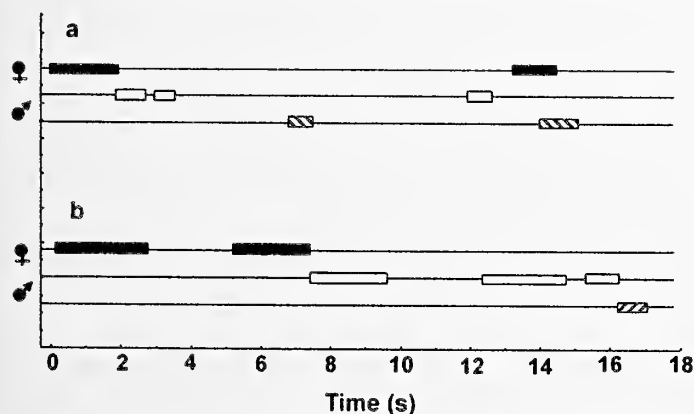
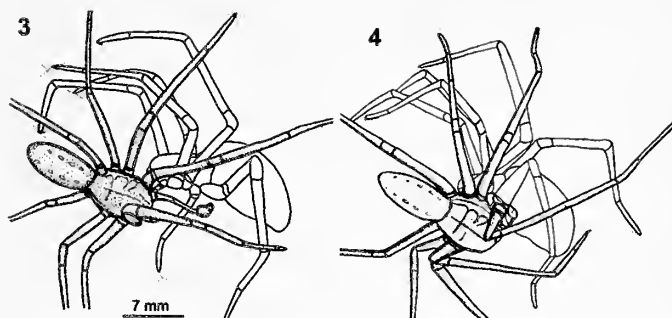


Figure 2.—Two partial sequences (a and b) of male-female courtship. Black boxes- female strumming movements, Empty boxes- male rocking movements, Dashed boxes- male moving toward the female.



Figures 3, 4.—Position of male and female previous to and during insertion. 3. The female lays on her right side as the male walks over her body. 4. Male inserting his left pedipalp (embolus) in the left opening of the female's epigynum.

movements of the male's abdomen, and were similar to the abdomen bobbing movement of *Leucauge* (Eberhard & Huber 1998). The pre-copulatory and copulatory courtship behaviors of a male after subsequent copulations on opposite sides were similar (e.g., flubs: 19-15-16; three subsequent copulations). The extremely short insertions were successful as one of the females produced fertile eggs. The insertions seemed to be ipsilateral (by the position of the female's epigynum and male's palp), although I could not be completely certain due to the dark color of the epigynum and male's palp.

The female terminated copulation when she began to move her legs to stand on the sheet after a single successful insertion of the male's palp ($n = 5$) or after several unsuccessful insertion attempts of the male's palp ($n = 4$) (I could not differentiate unsuccessful insertion attempts from flubs). In one case the male remained over the female and she darted toward him in an attacking position. The female's attack provoked an extremely rapid backward movement by the male that positioned him at 3 or 4 cm from her. After the female had ended the copulation, the male began a new approach with a sequence of pre-copulatory courtship behaviors. The courting male stopped frequently to pass his palps and sometimes his legs through his mouthparts before approaching her again; occasionally the male rubbed his palps against the sheet after grooming his palps with his chelicerae. During each new male approach, the female inclined her body toward the opposite side as the male walked over her and he immediately began to contact her epigynum with his other palp. Successive inclinations and insertions were on opposite sides ($n = 12$) except when the male failed to insert his palp in the previous attempt. In such cases the next male approach occurred on the same side of the female side that he had approached previously. The female was apparently responsible for the alternation of sides in subsequent copulations; it was clear on two occasions that she began to incline her body before the male could contact her.

Having copulated, the female did not necessarily accept the male the next time he approached her. On several occasions (10 in one pair and 4 in the other) the male stopped his approach as she began to strum the sheet, and he restarted his rocking courtship behavior. Neither male charged his palps with sperm during the courtship, indicating that males charged their palps before encountering a female.

The male's pre-copulatory rocking and abdominal bobbing movements during copulation may reduce the female's aggression and induce her to cooperate and use his sperm to fertilize her eggs (Eberhard 1996; Stratton et al. 1996; Eberhard & Huber 1998; Peretti et al. 2006). It is possible that these movements inform the female of the male's quality. For example, one of the females of this study immediately lunged at and expelled from the web a small adult male (ca. 15% shorter than the males studied) that I had previously placed on her web.

The strumming behavior of the female, her ability to expel males with her attacks, and assumption of a distinctive acceptance posture, all clearly show her active role in mating (Peretti et al. 2006). This behavior possibly serves the female as a criterion for male selection as it induces the male to restart, and in some cases, seemingly to intensify his courtship behavior after he detects a female strumming. As in many other spiders, there was no indication of males being able to force females to cooperate (Huber 1996; Eberhard & Huber 1998).

It is possible to compare some aspects of the courtship behavior of *T. radiata* with that of species of other related families: Agelenidae, Lycosidae and Pisauridae (Coddington 2005). In all these families, including *T. radiata*, males mount females facing in the opposite direction (Nielsen 1932; Miller & Miller 1987; Hebets et al. 1996; Stratton et al. 1996; Huber 1998; but see Bruce & Carico 1988). However in *T. radiata* the male's courtship induces the female to incline her body to expose her epigynum, and thus his ventral surface touches (or nearly so) the ventral surface of the female, while in wolf spiders the male's ventral surface touches the dorsal surface of the female and the male's pedipalp reaches the female's epigynum around the side of her abdomen. In at least some lycosids (Stratton et al. 1996) and in several agelenids (Huber 1998) males also flub ("scrape" in Stratton et al. 1996) repeatedly prior to insertions. Copulations involve ipsilateral palpal insertion on alternating sides in all families (Stratton et al. 1996). Alternating insertions with only a single expansion of the hematodocha also occurred in *Rabidosa* spp. (Lycosinae) (Stratton et al. 1996). Female attack behavior similar to that of *T. radiata* occurs in one lycosid (Miller & Miller 1987) and one pisaurid (Arnqvist 1992). Many of these behaviors are possibly homologous with those of Tenggellidae, but information about many more species is required to make stronger arguments regarding the evolution of courtship behavior in *Tenggella* and related families. Particularly, the information on courtship behavior of agelenoids, the sister group of Tenggellidae and lycosoids, is very important to trace the evolution of the courtship behavior in these groups of spiders.

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SHORT COMMUNICATION

Snatching prey from the mandibles of ants, a feeding tactic adopted by East African jumping spiders

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Abstract. Instances are documented of salticids robbing ants by adopting a specialized behavior pattern, “snatching.” The salticid positioned itself beside an ant column on the wall of a building, repeatedly fixating its gaze on different individual ants in the column and maintaining fixation on the ant by turning its body while the ant walked by. When close to an ant that was carrying prey, the salticid maneuvered about so that it was head on, grabbed hold of the prey using its chelicerae, and then rapidly pulled the prey out of the ant’s mandibles. Having secured the prey, the salticid moved away from the ant column to feed. All observations were made at Mbita Point, by the shore of Lake Victoria in western Kenya. The salticids were three species of *Menemerus* (Simon 1868): *M. bivittatus* (Dufour 1831), *M. congoensis* Lessert 1927 and an undescribed species, *Menemerus* sp. n. The ant species were from the genera *Crematogaster* (Lund 1831) and *Campopnotus* (Mayr 1861). In all instances, the salticid was 2–6 mm in body length (juveniles of all three *Menemerus* species and adults of *Menemerus* sp. n.). Prey items taken from ants were, in most instances, “lake flies” (adults of Chaoboridae and Chironomidae).

Keywords: Salticidae, ants, predation, stealing prey, Chironomidae, Chaoboridae

In the tropics, ants (Formicidae) are the dominant insects (Hölldobler & Wilson 1990) and jumping spiders (Salticidae) are the dominant spiders (Coddington & Levi 1991), but we are only beginning to understand how salticids and ants interact (Nelson & Jackson 2005, 2006a,b; Nelson et al. 2006). Salticids are unique among spiders because of their complex eyes (Land 1969; Blest et al. 1990), exceptionally acute vision (Land & Nilsson 2002) and intricate vision-guided predatory behavior (Jackson & Pollard 1996; Harland & Jackson 2004). Most species in this large family (about 5,000 described species, Platnick 2008) appear to be active hunters that prey primarily on a variety of insects, but typically they do not prey on ants. It may not be surprising that many salticid species can detect ants by sight and then avoid coming close to them (Nelson & Jackson 2006c), particularly considering the formidable defences shown by ants (Blum 1981; Hölldobler & Wilson 1990), including powerful mandibles, poison-injecting stings and formic-acid sprays, and the fact that ants are sometimes predators of salticids (Nelson et al. 2004).

Yet there is a large minority of salticids (the “myrmecophagic species”) that selects ants as preferred prey (Li & Jackson 1996; Clark et al. 2000; Jackson & Li 2001; Huseynov et al. 2005) and one salticid species, *Cosmophasis bitaeniata* (Keyserling 1882), is known to combine chemical ant mimicry with myrmecophagy (Allan & Elgar 2001) (i.e., by mimicking the cuticular hydrocarbons of the Australian weaver ant, *Oecophylla smaragdina* (Fabricius 1775), *C. bitaeniata* gains entry to the weaver ant’s nest and feeds unmolested on the ant’s larvae). Here we revisit a different style of exploiting ants — robbing ants of objects they carry in their mandibles. This was first described by Bhattacharya (1936) who observed juveniles of *Menemerus bivittatus* (Dufour 1831) (formerly *Marpissa melanognathus*) in India grabbing food out of the mandibles of fire ants, *Solenopsis geminata* (Fabricius 1804). Our own observations show that this tactic, which we will call “snatching from ants” or just “snatching,” for short, is unique neither to India nor to *M. bivittatus*. The baseline information we provide here is a step toward later quantitative and experimental research concerned with this poorly understood foraging method.

METHODS

Menemerus is a large, well-defined genus, probably with many of the African species yet to be described (Wesolowska 1999). Our observations were on *M. bivittatus* (Dufour 1831), *M. congoensis* (Lessert 1927) and a new, undescribed species, *Menemerus* sp. n. all three of which are common in East Africa (see Jackson 1986, 1999). Typical body lengths of adult females of each species are: *M. bivittatus*, 10 mm; *M. congoensis*, 7 mm; *Menemerus* sp. n. 5 mm. Voucher specimens of all species from this study (salticids, ants, and prey) have been deposited with the Florida State Collection of Arthropods in Gainesville and the National Museums of Kenya in Nairobi.

Our study site was by the shore of Lake Victoria in western Kenya (Mbita Point, the Thomas Odhiambo Campus of the International Centre for Insect Physiology and Ecology). Mbita Point is 1200 m above sea level (0°25'S–0°30'S, 34°10'E–35°15'E) and has a mean annual temperature of 27° C. In this habitat, midges (Diptera: Chironomidae & Chaoboridae), known locally as “lake flies,” are exceedingly abundant (Beadle 1981), often covering the walls of buildings. As midges have notoriously short life spans, lake-fly swarms quickly turn into enormous numbers of lake-fly corpses which are routinely scavenged by ants.

We opportunistically observed *Menemerus* and other salticids when they were seen in the vicinity of ants on building walls. Whenever we saw a salticid persistently orienting toward an ant (identified to genus only), we continued observation for 30–60 min or until the salticid secured the prey. First we made about 30 preliminary observations of *Menemerus* sp. n. snatching lake flies from an unidentified species of *Crematogaster* (Lund 1831), but with no attempt made to identify the lake fly to family and no records kept concerning the salticid other than the species to which it belonged. We videotaped 10 of these preliminary observations for more detailed information about behavior.

This was followed by observations ($n = 98$) that were more standardized with respect to the information we recorded. After each of these observations, we collected the salticid, the ant and the “prey” (i.e., object snatched from an ant). Salticids were identified to species,

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ants to genus and lake flies to family. We also recorded whether the salticid was a juvenile or an adult, and we recorded whether adults were male or female. Earlier convention (Jackson and Li 2001) is adopted for indicating frequencies of occurrence: "usually," "often," "typically," and "typical" indicate ca 80% or more.

RESULTS

Snatching from ants.—The three *Menemerus* species, as well as *Evarcha culicivora* (Wesolowska & Jackson 2003), *Harmochirus brachiatus* (Thorell 1877), *Hasarius adansonii* (Audouin 1826) and unidentified species of *Hyllus* (Koch 1846), *Natta* (Karsch 1879), *Myrmarachne* (MacLeay 1839), *Plexippus* (C.L. Koch 1846), and *Thyene* (Simon 1885), were common on the walls of buildings, with many other salticids present in smaller numbers. However, only the three *Menemerus* species were observed snatching from ants.

In the records of salticids snatching from ants ($n = 98$), salticid body length varied from 2 mm ($n = 1$, 1%, *Menemerus* sp. n.) to 6 mm ($n = 1$, 1%, *M. bivittatus*), with 6 (6%) being 3 mm, 27 (28%) being 4 mm and the majority ($n = 63$, 64%) being 5 mm. For the majority records of snatching from ants ($n = 98$), the salticid was *Menemerus* sp. n. (78, 80%), with 58 (74%) of these 78 records coming from adult females, 6 (8%) coming from adult males, and 14 (18%) coming from juveniles. For all records for *Menemerus congoensis* ($n = 10$, 10% of 98) and *M. bivittatus* ($n = 10$, 10%), the salticid was a juvenile. The ants were undetermined species from the genus *Crematogaster* ($n = 72$, 73%) and *Caulponotus* (Mayr 1861) ($n = 26$, 27%).

Observed snatching sequences took place either in the morning (07:00–11:00 hours, $n = 75$) or in the late afternoon (17:00–19:00 hours, $n = 23$). The objects snatched from ants were usually (90, 92% of 98) dead lake flies (body lengths: 5 to 10 mm) (chironomid, $n = 77$, 79% of 98) and chaoborid ($n = 13$, 13%). Besides lake flies, adult females of *Menemerus* sp. n. (body length 5 mm) were also observed snatching an ant egg ($n = 1$), a dead mayfly (Ephemeroptera, $n = 1$), a dead *Crematogaster* worker ($n = 3$) and what appeared to be plant material ($n = 3$), with all of these objects being comparable to lake flies in size. *Menemerus* sp. n. subsequently ate the mayfly and the ant egg, but released and moved away from the plant material and the dead ant a few seconds after contact. There were also five instances in which *Menemerus* sp. n. (3 adult females and 2 juveniles) snatched a dead lake fly (not identified to family) from an ant and then, a few seconds later, released the lake fly and walked away. In all other instances, the salticid ate the lake fly it snatched from an ant.

Behavioral sequences were similar irrespective of the different prey, ant genus, *Menemerus* species and, for *Menemerus* sp. n., whether the salticid was a juvenile, an adult male, or an adult female. Five behavioral stages were discerned: tracking, intercepting, attacking, retreating, and feeding.

Tracking: a salticid positioned itself beside an ant column on the wall of a building, repeatedly fixating (i.e., aligning the gaze of the corneal lenses of its anterior-medial eyes) on different individual ants active in the column and maintaining fixation on each ant for 5 s or longer by continually turning its body while the ant walked by. The ant being tracked was usually carrying an object in its mandibles. The salticid usually remained 50–100 mm from the ant while tracking and stepped out of the way whenever an ant turned and moved in its direction.

Intercepting: a spider that had been tracking suddenly began stepping about and maneuvering into position in front of the ant, effectively blocking the ant's forward progress. This usually happened only a few seconds after the salticid was first seen tracking, as any longer delay usually resulted in the ant moving far away from the salticid. When intercepting, *Menemerus* usually took a veering path and approached the ant column 20–45° off from straight ahead of the targeted ant's forward trajectory. When *Menemerus* stepped in front

of the ant, the ant either stopped momentarily before moving off in a different direction or it just slowed down and veered to the side, with *Menemerus* continuing to maneuver itself in front of the active ant.

Attacking: during one of an ant's momentary pauses when being intercepted or else while the ant was attempting to step out of the way, a spider suddenly extended its rear legs, moved its body 1–2 mm forward, brought its chelicerae into contact with an object in the ant's mandibles and then immediately stepped a few millimeters backwards or to the side, pulling the object out of the ant's mandibles. In all instances, the ant released the object when the salticid pulled away.

Retreating: after extracting an object from the ant's mandibles, the spider turned and rapidly walked away, usually not stopping until about 100–200 mm from the ant column.

Feeding: the spider settled, usually in a space between bricks or in some other secluded location on the wall, and then proceeded to feed for 1–10 min. After feeding, the spider dropped the prey and walked away, after which it often returned to the ant column and stole another lake fly from the ants. As many as four lake flies were sometimes stolen in succession.

There were about 10 instances each for *M. congoensis* and *M. bivittatus*, and more than 40 for *Menemerus* sp. n., in which we observed a salticid briefly tracking an ant that had empty mandibles, but we never saw a salticid intercept these ants. There were also about 30 instances in which *Menemerus* sp. n. briefly tracked, but then failed to intercept, as well as 9 instances of seeing a salticid track and then intercept an ant that was carrying an object other than a lake fly, but then move away without attacking (*Menemerus* sp. n., 5 ants carrying plant material and 2 carrying a dead conspecific ant worker; *M. congoensis*, 2 carrying dead conspecifics).

DISCUSSION

Bhattacharya (1936) provided minimal descriptive detail of snatching behavior. He did not indicate how many times he observed *M. bivittatus* snatching from ants and he referred to the objects *M. bivittatus* stole as simply "food and eggs" (ant, spider, and object sizes not indicated). Yet his observations on *M. bivittatus* in India appear to have been similar to ours: tracking, intercepting, attacking (pulling the prey out of the ant's mandibles) and retreating with the prey before feeding.

Bhattacharya (1936) also observed *M. bivittatus* adults, but not juveniles, stalking, capturing, and feeding on house flies, *Musca domestica* (Linnaeus 1758) and he suggested that snatching prey from ants might be the primary foraging tactic of *M. bivittatus* juveniles. We hesitate to suggest that this is the primary tactic used by any of the active stages of any of the three *Menemerus* species we studied because we observed all stages of each of the three *Menemerus* species frequently capture and eat free (i.e., not in the mandibles of ants) living prey by practicing the stalk-and-leap routines that appear to be typical of many salticid species (Forster 1982; Richman & Jackson 1992; Jackson & Pollard 1996).

Our observations suggest instead that snatching from ants is an alternative foraging tactic sometimes adopted by small individuals (i.e., individuals no more than 6 mm in body length) of *Menemerus*. For the smallest of the three *Menemerus* species we studied (i.e., *Menemerus* sp. n.), this included adults of both sexes as well as juveniles. However, for *M. bivittatus* and *M. congoensis*, this included only juveniles.

Despite many salticid species being abundant at Mbita Point, the only salticids we saw snatching prey from ants were the three *Menemerus* species. These observations from East Africa, together with Bhattacharya's (1936) records from India, suggest that snatching from ants may be widespread among species of *Menemerus* living in ant-rich habitats. Further work is needed for determining whether this tactic is special to the genus *Menemerus* and for clarifying the selection pressures that might have favored the evolution of snatching behavior.

It is difficult to envisage a salticid needing an ant's help overpowering inoffensive, soft-bodied lake flies and seeing building walls on the shore of Lake Victoria covered by lake flies does not suggest that finding lake flies is a pressing problem for which a salticid might need an ant's assistance. We may be tempted by an image of salticids grazing on clumps of lake flies, rather like antelopes grazing on clumps of grass, but choosing and capturing a living lake fly may be far from effortless for a salticid. Time considerations may be important. Success for *Menemerus* during stalk-leap sequences may often depends on slowly moving close enough to gauge an accurate leap, with a targeted prey potentially nullifying the salticid's efforts by flying away. Stalking sequences typically take several minutes, compared with the few seconds needed to intercept an ant.

Decision making is another potential problem for a salticid. The image of unlimited lake-fly prey changes somewhat upon close examination. Many of the lake flies covering building walls are in fact already dead, but stray silk lines left by spiders hold dead lake flies in place in lifelike postures on the wall. A light breeze often makes the dead lake flies twitch and jiggle about. *Menemerus* and other salticids were often seen stalking these dead flies, leaping on them when close and then almost immediately releasing them, but there were only five instances in which we observed *Menemerus* sp. n immediately release and move away from a dead lake fly it had snatched from an ant. Perhaps one of the primary advantages of stealing from ants is that the salticid can rely on the ant to select lake flies that are still fresh enough to be palatable.

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SHORT COMMUNICATION

Excretion behavior of adult female crab spiders *Misumena vatia* (Araneae, Thomisidae)

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Abstract. Excreta potentially provide parasites or predators with information about the presence of hosts or prey; hence, vulnerable individuals experience strong selection to minimize danger from this source. Alternatively or additionally, excreta could alert potential prey to a spider's presence. Adult female crab spiders *Misumena vatia* (Clerck 1757) exhibited a strong reluctance to excrete when retained under tightly confined conditions. Only 5% of regularly fed individuals (1% of total observations) excreted over observation periods of as many as 50 days while confined in 7-dram vials (5 cm high, 3 cm diameter). Individuals retained large amounts of excreta during this time. However, when released upon vegetation over two-thirds of them excreted within 5 min, after moving to the distal end of a leaf or petal such that the excreta fell below them onto lower vegetation or the substrate. In the field they showed little tendency to excrete close to their hunting sites. The ability to retain excreta should serve this relatively sedentary species well in situations where it suffers high rates of attack or may reveal its presence to potential prey.

Keywords: Defecation, parasite avoidance, predator avoidance, retention behavior

Many animals may experience risks in voiding excretory material, which likely enhance the possibility of alerting predators and parasites to their presence and increase the danger of disease. Alternatively or additionally, the presence of excreta could forewarn potential prey to a predator's presence. Considering the importance of these factors, surprisingly little attention has focused on studies examining the responses of predatory invertebrates to host or prey waste products (Weiss 2006). In particular, workers have written little about excretion in spiders (Curtis & Carrel 2000) or other arachnids (Sato et al. 2003; Sato & Saito 2006). In fact, Curtis & Carrel (2000) believed their paper on excretion behavior by garden spiders *Argiope aurantia* Lucas 1833 (Araneidae) (referred to as defecation behavior by the authors) to be the first explicit study of its sort on a spider, although Tietjen (1980) reported on the nonrandom distribution of excreta under laboratory conditions in *Mallos gregalis* (Simon 1909) (Dictynidae). Throughout this paper I use the term "excretion" (excreta, excrete, etc.) to identify the materials passing through a spider's anus, since the majority of this material consists of the products of post-assimilatory metabolic processes from the Malpighian tubules, rather than undigested matter.

In response to the risk of this material providing cues to their presence, potential prey or hosts might develop behavioral responses that minimize this threat, such as excreting away from their normal activities or retaining excreta indefinitely until they can safely void them. Taxa that show high fidelity to a site should experience particularly strong pressure to develop such tactics, as demonstrated by Weiss (2003, 2006) for caterpillars.

Crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae) typically occupy flowers as sit-and-wait predators of insects and in the process may often remain at hunting sites for several days at a time. Excretion in these areas could attract a large number of predators and parasites through either visual or olfactory cues provided by this material. Although various vertebrates are usually considered the most common predators of spiders, they only infrequently prey on *Misumena* in coastal Maine, where I conducted this study (Morse 1985, 2007). More important are other invertebrates, especially spiders, predatory wasps, and parasitoid wasps and flies (Morse 1988a, 1988b), some of which likely respond to olfactory cues.

Here I characterize the excretion behavior of adult female *Misumena* retained for extended periods under confined conditions and then provided with sites that allowed them to dispose of their

excreta some distance away from their hunting sites. I quantified the spiders' frequency and size of excretion when confined to small vials and immediately following their release onto vegetation, both flowers in the laboratory and leafy vegetation in the field. I also report observations on the excretion patterns of free-ranging adult females in the field. In combination, these results allow me to test whether these spiders discriminate among potential excretion sites, whether the spiders' ability to separate themselves from their excreta affects which sites they use for this purpose, and whether the site affects the size of the excretion.

METHODS

Adult female *Misumena* are medium-sized spiders that molt into the adult stage at 35–60 mg and may exceed 400 mg when they lay their single egg mass. These spiders have two large, raptorial anterior pairs of legs and two much smaller posterior pairs. They can change their color between white and yellow, and most have a prominent pair of deep red dorsolateral abdominal stripes.

Misumena frequent old fields and roadsides in my study area (South Bristol, Lincoln County, Maine, USA), where they hunt on flowers for large prey. I collected 72 adult females from these sites in June and July for studies unrelated to this one. The design of that work dictated in part the types of observations that I could make for this study. I kept the spiders in 7-dram vials (5 cm tall, 3 cm diameter) at ambient temperature and light regimes and fed them a moth (Noctuidae, Geometridae) or large fly (Syrphidae, Muscidae) every other day. Adult female spiders grew rapidly on this diet and did not require supplementary liquids. In the process I retained individuals for several days to well over one month. Retention times of the spiders varied in accordance with their mass upon capture and how rapidly they gained mass up to the point of egg laying. I recorded excretions when feeding the spiders and cleaning their vials after feeding or excretion. I did not start recording retention times of excreta by the spiders until they had been in the vials for two days to ensure that all individuals were in a similar hunger state. These spiders will usually take a large prey item every other day (Morse & Fritz 1982). Numbers of drops of excreta were counted whenever possible.

For the laboratory observations, I released female *Misumena* from their vials onto a flower, either an oxeye daisy *Chrysanthemum leucanthemum* or black-eyed Susan *Rudebeckia hirta*, and observed

their behavior. I then counted all excretions produced within the next five minutes. Previous observations had demonstrated that the females often excreted immediately after release on a flower, particularly if I had retained them for several days before release (D.H. Morse, unpub. obs.).

I placed another group of previously confined adult females in the field on young, non-flowering milkweed *Asclepias syriaca* plants, sites previously recognized as favored nesting places (Morse 1985). Upon releasing spiders onto the plants, I observed these individuals for five minutes to determine whether they would excrete during that period, since earlier unrelated observations had established that they often excreted within this time.

I also tested the frequency with which free-ranging adult female *Misumenina* excreted in conspicuous hunting sites on wild marjoram *Origanum vulgare* over periods as long as 17 days. These marjoram stems averaged 0.5 m in height and grew densely at the test site, which contained several hundred flowering stems. They bore terminal rounded panicles composed of multiple small pinkish-purple flowers. Immediately below their inflorescences marjoram stems bear dense ovate leaves, such that the hunting sites in marjoram occur in the top of a dense canopy of flowers and leaves. This situation made it difficult for spiders to excrete from their hunting sites without soiling nearby vegetation.

RESULTS

Characteristics of behavior and excreta.—*Misumenina* exhibited distinctive excretion behavior: individuals moved to the tip of a petal or leaf, raised themselves on their two pairs of large forelimbs, the two smaller pairs of posterior limbs usually not contacting the substrate at this time, and then released varying numbers of drops of a whitish liquid with dark brown flecks that quickly dried in the air to a dirty light brown. Upon release onto the flowers the spiders typically commenced excretion behavior quickly, often within the first 30 seconds. In the laboratory, excretions made from the tips of flower petals fell onto the substrate below; in the field they most often completely cleared the plant in question, landing on the grass in the substrate. When voided from milkweed leaves in the field, the excreta most often landed on another leaf of the plant below the excretion site. If permitted to climb to the rim of their vial the spiders readily excreted from there as well, exhibiting the same behavior as seen on the petals and leaves (D.H. Morse, pers. observ.).

During large excretions in which the spiders voided many drops, they released most of these drops in a nearly constant stream, so that my counts of these drops were approximate. These excretions averaged $5.0 \pm 0.97\%$ (\pm SE, $n = 6$) of the previous body mass (D.H. Morse, unpub. data). The spiders distinctly spaced these drops in smaller excretions.

Tendency to excrete.—I recorded only four excretions in the vials during the feeding and cleaning sessions that took place every second or third day. These involved 72 spiders and 335 observations of spiders at these sessions, with spiders present for 1–15 such sessions (5.6% of the spiders and 1.2% of the total observations showed excretion). I did not retain most individuals long enough to obtain probable maximum retention times of excreta, but individuals regularly refrained from excreting for up to one month or more, with a maximum of 47 days. Unfortunately I failed to record which individuals excreted, but even if one assumes that the four longest-remaining individuals (47, 39, 39, 35 days) excreted, thereby accounting for the four excretions recorded during this period, seven individuals retained their excreta for over 30 days [34 (2), 33 (4), 32 (1)]. Thus, individuals could routinely retain their excreta for long periods.

In laboratory observations, 29 (67.4%) individuals excreted during the five-minute period after release from the vial, and 14 failed to excrete at this time. This result differed highly significantly from the number expected from the spiders' behavior in the vials, which would

predict zero or one excretion ($G = 40.51$, $df = 1$, $P < 0.001$ in a G -test for goodness of fit). None of these individuals excreted in subsequent minutes. When released on the milkweed plants, 28 (73.7%) individuals excreted within five minutes, and 10 did not excrete, a highly significant difference, using the same rationale as the previous test ($G = 55.39$, $df = 1$, $P < 0.001$, same test).

Size of excretions.—Excretions, measured as drops of liquid, differed widely in volume, probably a consequence of how long individuals had retained this material. In the laboratory sessions excretions averaged (\pm SE) 6.6 ± 1.50 drops, range = 1 to 26 ($n = 22$ observations); on the milkweeds they averaged 9.0 ± 1.62 drops, range = 1 to 24 ($n = 18$ observations). Excretions at release in the field significantly exceeded those during laboratory sessions ($U = 130.5$, $P < 0.03$ in a one-tailed Mann-Whitney U test). On average, retention of excreta at release should exceed those recorded in the laboratory.

The size of excretions at release was positively related to the time that spiders had retained this material ($R^2 = 0.41$, $n = 17$, $P < 0.01$). In contrast, no relationship occurred between the size of excretions of individuals in the laboratory sessions and their retention times ($R^2 = < 0.01$, $n = 15$, $P > 0.9$, same test).

Behavior in the field.—During six censuses run every third day on marjoram, I made 45 observations of the free-ranging spiders out of a possible 120 (number of spiders released \times number of counts). I observed a maximum of 11 spiders during a census, although recording 18 of them during one census or another (mean \pm SE = 7.5 ± 0.96 individuals). As a result, these spiders might have spent as much as 62.5% (75 of 120 possible observations) of their time away from hunting sites, and a minimum of 27.5%, based on unrecorded individuals later found in the flowers (33 instances). These absences would provide ample opportunity for the spiders to excrete unnoticed. In the process of this census I failed to find a single excretion in the vicinity of a hunting site.

DISCUSSION

Adult female *Misumenina* often retain their excreta for long periods under experimental conditions, a trait that should help to facilitate their relatively sedentary behavior. Since these spiders often remain for several days at a time on a superior hunting site (Morse & Fritz 1982), they should experience strong selection to void their excreta carefully. Seldom if ever did the location of such an individual become conspicuous in the field (at least to the human eye) as a result of their disposition of excreta (D.H. Morse, unpub. observ.), including the explicit observations reported here. Spiders possess a large stercoral pocket (cloacal chamber) with a muscular sphincter that allows them to store large amounts of excreta (Seitz 1987).

The clear difference in relationship between size of excretion and time confined accords with the spiders excreting more regularly in the field than under confined laboratory conditions. Under these circumstances the individuals tested upon release in the field would have gone longer without excreting than those measured earlier in the laboratory, and hence, since fed regularly, would have accumulated significantly more excreta. Less likely, they might simply void less prior to the experiments, though I have no basis to support this alternative. Curtis & Carrel (2000) reported that garden spiders fed mealworms excreted over twice a day under otherwise normal field conditions.

The spiders hunting on marjoram would have had little opportunity to excrete without soiling nearby vegetation if they had remained on their hunting sites. They might excrete low in the vegetation without my detecting them. Such behavior would match other observations suggesting that the spiders excrete more readily at sites where the excreta fall far below their hunting areas than where the excreta would fall in their midst (D.H. Morse, unpub. observ.).

Dropping excreta from their immediate vicinity to the vegetation beneath them should make the spiders more conspicuous to other

animals on or near the substrate than to those in the canopy or above it. However, dropping their excreta away from their canopy-level hunting sites should make the spiders less vulnerable to most winged attackers, probably the most important threats to spiders in the leafy canopy. When they venture down onto the grassy substrate they expose themselves to attacks from such predators as meadow voles *Microtus pennsylvanicus* and garter snakes *Thamnophis sirtalis* (Morse 1985). In the canopy the egg predator *Trychosis cyperia* (Ichneumonidae) is their most important threat (Morse 1988b). In all of my observations on *Misumena*, I have never seen them preyed upon by birds (Morse 2007); however, the spider wasp *Dipogon sayi* (Pompilidae), rare in the study areas, takes a very occasional small adult female (two observations: D.H. Morse, unpub. data), and large sphecids wasps (Sphecidae), also uncommon in the study areas, are other potential predators, especially of penultimates (Morse 2007).

I have little information on the role of disease or internal parasites, factors that should also favor careful disposition of excreta. I have twice reared horsehair worms (Gordioidea) from adult females (D.H. Morse, unpub. data), but these events are relatively rare, since the two records come from a sample of several thousand females collected in the field as adults or penultimates. Tietjen (1980) reported little sign of bacterial or fungal growth about excreta of *Mallos gregalis*. Behavioral traits, however, may play an important role in controlling levels of parasitism of other animals (e. g., Hart 1992; Ezenwa 2004).

Other sparse information on the excretion behavior of spiders suggests that they minimize the apparency of their excreta at their normal hunting level in the vegetation. Curtis and Carrel (2000) noted that the garden spider often leaves its web to excrete, and that it generally does so at night; however, it excretes under its web, consistent with their impression that its major predators are birds and predatory wasps. *Mallos gregalis* concentrated its excreta in parts of an experimental enclosure that it used least frequently (Tietjen 1980). Bonnet (1930) reported that the fishing spider *Dolomedes fimbriatus* (Pisauridae) forcibly cast its excreta out from as far as 3–4 cm from its body. It also frequently excreted before jumping into the water, which could divert a would-be predator, as suggested by Seitz (1987). Although typically presented in the context of predator avoidance, some results may equally well minimize apparency of the spiders to prospective prey, as described by Brown et al. (1995) for pike-minnow interactions. I am unaware of any instances in which excretion patterns of spiders can be unequivocally attributed to minimizing apparency to prey, though this relationship might obtain in many instances, perhaps simultaneously with predator or parasite avoidance. Taken together, these observations, in combination with those of *Misumena* reported here, all suggest that distinctive patterns of excretion behavior may be widespread, but frequently ignored, among spiders.

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